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BEHAVIORAL PATTERNS RELATING TO AGE AND SEX IN FREE-RANGING SPIDER MONKEYS (ATELES GEOFFROYI) IN TIKAL NATIONAL PARK, GUATEMALA

BY

© MARGARET JOAN BAXTER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF ARTS

DEPARTMENT OF ANTHROPOLOGY

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled BEHAVIORAL PATTERNS RELATING TO AGE AND SEX IN FREE-RANGING SPIDER MONKEYS (Ateles geoffroyi) IN TIKAL NATIONAL PARK, GUATEMALA submitted by Margaret Joan Baxter in partial fulfilment of the requirements for the degree of Master of Arts.

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Date December 4, 1978

ABSTRACT

A population of free-ranging spider monkeys (*Ateles geoffroyi*) was observed for six months in Tikal National Park, Guatemala. Previous studies of *Ateles* populations have been concerned with general types of ecological explanations of *why* various observed patterns of social behavior are occurring. In this study the aim was to ascertain *how* the social system of *Ateles* was maintained, by looking at the structural principles operating within it. The focus was on the social interactions and behavioral profiles of individual monkeys who were identified according to their age and sex. Following Hinde (1974, 1976) social interactions were felt to be indications of underlying social relationships between and within age-sex classes. Of interest were the kinds of relationships which structure social networks within the localized population of spider monkeys at Tikal. Special attention was paid to the degree and nature of separation between the behavioral profiles of males and females.

Sex roles in spider monkeys are discussed with reference to some broad generalizations which are predominant in the literature dealing with sex differences in primates. Spider monkeys were found not to conform to some of these generalizations about male and female behavior in multimale groups; generalizations which have developed mostly from studies of specific multimale systems found in Old World

species such as macaques and baboons.

It was found that adult males maintained strong affinitive relationships with other adult males. The relationships between adult males and adult females also showed mutual affinity, but adult males directed frequent intimidating agonistic chases at adult females. Intertroop displays which may have defined troop territories and maintained spacing of localized populations, were performed by adult males.

Adult females tended to maintain looser networks of relationships with all age-sex classes. However, they were most consistently in association with other adult females, juvenile females, and mothers and infants. The larger loose groups of females in association with mixed age-sex classes underwent frequent fusion and fission during the day. Smaller units of monkeys dispersed in the course of their daily foraging activities, and periodically aggregated for periods of rest and sleeping. Units of females with young apparently maintained vocal contact with others at times of dispersed foraging. In addition, adult females performed a ritualized vocal display which was observed during times of high tension in the troop. This behavior may have been a response to potential sources of danger such as that of predators or human presence.

The development of sex differences was examined by looking at the actions and interactions of juvenile and infant monkeys. Young males tended to interact less with

their natal groups and more with adult males than did young females. Strong affinitive relationships were found to exist between adult and juvenile females. Mothers directed relatively more care-taking activities toward infant females than toward infant males.

Finally, social relationships between and within age-sex classes and behavioral profiles of each class are discussed as elements comprising the social system of spider monkeys at Tikal. While the social organization of spider monkeys is seen as a product of stable structuring principles, it is viewed as a system with built-in flexibility. This flexibility has also been viewed as adaptive for frugivorous monkeys living in an arboreal habitat.

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CHAPTER ONE

INTRODUCTION TO THE PROBLEM

According to Mason (1976), two kinds of questions have shaped the approaches taken by field workers in their collection and analysis of data, and their subsequent interpretation of primate social behavior. On one hand there has been a focus on various social structures as products of selective forces. This approach looks at many aspects of primate social systems, such as observed patterns of grouping, and relates them to specific ecological parameters, with attention to their 'functional' significance. It is the functional approach which characterizes the field studies made to date of spider monkeys (genus Ateles). For example, Klein (1972) viewed fluctuating and flexible group compositions of Ateles belzebuth in Colombia as functions of food (fruit) availability, its distribution and dispersion in trees, and its seasonality. His socio-ecological study was concerned with why the observed grouping patterns were occurring, and he looked at these social patterns as adaptive feeding strategies.

Secondly there is an approach which aims at answering questions of causation; how monkeys are organized within groups and the social system as a whole (Mason 1976). The focus is on the internal structure of the groups, and the social principles which maintain the social structure. Drawing on concepts from the social sciences, Hinde (1974,

1976) and Hinde and Stevenson (1976) presented a conceptual framework for performing a causal analysis of primate social structure. They delineated three levels for analysis: (1) social interactions are basic elements of social structure, (2) social relationships involve a succession of social interactions between individuals, and (3) the social structure of a group can be described in terms of the nature, quality, and patterning of relationships (Hinde 1976). Each of these involves patterning of the elements in the level below it.

The earliest studies of primates often involved questions of <u>how</u> the groups were structured, and therefore early application of a 'causal' approach was made in studies of caged or captive primates where 'normal' social patterns and processes were frequently inoperative (Gartlan 1968). 'Normal' here refers to patterns of social behavior and structure (and the variation in these patterns) which characterized a species in feral populations. Such inappropriate application of the causal approach to primate social behavior gave rise to simplistic and inaccurate theories; sexual bonding or social dominance were the primary organizational principles behind nonhuman primate social structure (Gartlan 1968).

In recent years there has been an emphasis on field studies of primates, and the findings from such studies have shown that primate behavior is much more complex and variable than early studies of captive primates

had anticipated. It is now clear that we must look at questions of both how and why observed grouping patterns occur, if we hope to understand the extent of the complexity of primate social behavior.

While most field studies have focused on socio-ecological aspects of grouping patterns (functional questions), thus far the causal approach with its focus on individuals within the groups has been confined to the study of easily observed and well-habituated primate groups. Accordingly, terrestrial species such as macaques and baboons for whom we have genealogical data, precise group histories, and dominance charts, show that these groups are structured by highly complex internal processes, which would not have been revealed by a functional study of that group.

From such studies of terrestrial species, empirical data have been used to analyze the principles involved in the maintenance of group structure. Hinde (1976) details three groups of organizational principles which he feels are most important in producing social structure:

1. relationships between and within age-sex classes
2. blood (kin) relationships
3. status in the group

Using data which relate to each of these principles, a field worker is thus able to undertake a causal analysis of primate social structure.

Undertaking a causal analysis of social structure, utilizing all three of these principles, raises major

difficulties for the field worker dealing with arboreal primates, such as the spider monkey. This species lives in dense tropical forests through which it moves very rapidly in large flexible groups. Without a very long study, it is not possible to collect data that would lead to illumination of all three structural principles described by Hinde (1976). Therefore it is not surprising that a survey of the literature on spider monkeys in particular, and forest monkeys in general, reveals that our interpretation of their social structure has relied on analyses of primary ecological factors. Pervading the literature is the theme that the wide diversity in social structures which forest-dwelling primates exhibit is almost entirely a function of the diversity of the forest habitat (cf. Aldrich-Blake 1970, Crook 1970). It is generally agreed on the basis of preliminary studies, that social systems reflect, and are shaped by a particular mode of resource (Reynolds, cited in Kummer 1971: 45; Chivers 1974; Aldrich-Blake, cited in Crook 1970).

Initial studies of Ateles populations such as those by Carpenter (1935), Klein (1972), and Cant (1976) were concerned with general types of socio-ecological questions about various aspects of social organization. They suggested that correlations could be drawn between periodic dispersion and aggregation of the highly flexible groups of spider monkeys, and general patterns of food availability and distribution. The predominance of these studies may

have led to the inference that Ateles and other arboreal species are more simplistic and less highly developed than are some of their more widely studied primate counterparts; i.e., many Old World species for which social structure has been analyzed at the level of individual social roles. It is important that generalizations regarding behavior of primates, which are made on the basis of studies of only one species, are not applied a priori to less-studies species.

The purpose of this study is threefold. It aims:

1. To undertake a causal analysis of the social system of a free-ranging population of spider monkeys, by looking at how the social system is maintained.
2. To compare the results of this analysis of spider monkeys with some general patterns in other primate species where similar causal questions have been studied; such as sex roles in primate society.
3. To integrate the findings of this causal analysis of various aspects of the infrastructure of the social system, in a discussion of more functional descriptions of the adaptive value of the social system as a whole.

It is clear that studies must be made which take into consideration two major points. First, it is important not to make sweeping generalizations about the adaptive significance of basic social patterns.

> Answers to even the most obvious and fundamental questions such as why primates live in social groups and not as solitary individuals are usually couched in functional terms; for example, group life affords increased protection from predation (Kummer 1971)

> and hence, tells us little about the mechanisms by which individuals are attached to each other. (Kling and Steklis 1976: 216-217)

Secondly, a study which points to social grouping patterns as functions of rather general external pressures tends to brush over individual variability both within and between groups of the same species subjected to similar selective forces. Clutton-Brock states the problem this way:

> Functional aspects of more detailed behavioral differences and, in particular, of social relationships within groups, have still been largely ignored. . . much intra-group behavior is adapted to the social environment rather than to the external environment. (Clutton-Brock 1976: 195)

Hinde (1976) points out that stability of troop structure may be maintained in spite of environmental changes which may temporarily produce shifts in the patterns of relationships. Further, he says that since the structural stability survives both the birth and death of individuals and cyclic changes in group composition, we are safe in assuming that the troop provides an environment for the growing young such that they develop into individuals which form relationships akin to those formed by their elders (Hinde 1976: 11).

All aspects of social behavior can and should be broken down to consider advantages at the level of the individual (Eisenberg 1976). Selection operates to fit the social behavior of individuals to both the physical and social environment.

This study is concerned with the basic behavioral

repertoire, and it investigates the social infrastructure of the population of Ateles geoffroyi at Tikal, Guatemala. A month-long preliminary study of this population revealed that monkeys could be located fairly readily and that contact could be maintained with at least one individual for several hours. Sometimes it was possible to follow a single monkey as it moved through a day's activities, often in and out of visual contact with other monkeys.

As well, it was found that aging individuals as adult, juvenile, or infant was quite feasible; and that sex was also very easy to determine. Thus data collected on focal animals classified according to seven defined age-sex classes could be used to obtain behavioral profiles for each of these classes: adult male, adult female, juvenile male, juvenile female, infant male, infant female, and mother with infant. Data obtained by recording social interactions of individuals in each class, coupled with observations made of grouping tendencies and activity patterns, lend themselves to analysis of 'causal' questions about spider monkey social systems. The aim is to ascertain social relationships of spider monkeys at Tikal. These relationships are then related to the patterns of social structure for Ateles as they are described by previous researchers working with spider monkeys.

The specific aim of this (causal) study (of Ateles social behavior) was to obtain data which would either support or refute the following: The kind and amount of

social interaction between individuals are correlated with the ages and the sexes of the individuals involved. Discussion is focussed on how these behavioral patterns can be correlated with associative tendencies within and between these seven age-sex classes.

In addition this study discusses some general aspects of observed social behavior of the Ateles population at Tikal and in other areas. It has been shown that the structure of the spider monkey social system is characterized by great flexibility in grouping patterns (Klein 1972, Bramblett 1976). Previous studies of Ateles have identified the constantly fusing and fissioning groups as adaptations to the arboreal habitat and to frugivorous diets (Klein, 1972, Carpenter 1935, Freese 1976). This study attempts to illuminate structural principles within the groups which define the sources of stability and conversely, the normal limits of flexibility. It discusses the limits of flexibility of social behavior with reference to some generalizations which have been made regarding behavioral profiles for these age-sex classes in other primate species. These generalizations are summarized briefly in the following section, and later reassessed to lend perspective to a discussion of the results of this study.

CHAPTER TWO

REVIEW OF LITERATURE

Sexual Dimorphism and Sex Differences in Primate Behavior

Although the individual is the basic unit, or the building block of any primate society, the structure of the primate social system may be described in terms of the age-sex classes of the individual members (Itani 1977). The interactions in which individuals of each age-sex class engage are shaped by, and in turn shape, networks of social relationships within a primate group (Simonds 1974: 153). These networks of social relationships grow and develop with the individuals, and are ultimately both producers of and products of the social structure of the groups.

Thus an analysis which focuses on how and how much one monkey interacts with another, sheds some light on the internal structure of the social system, since it reveals both the relative strengths and the nature of these relationships. Stated explicitly:

> Every primate group shows a highly structured pattern of relationships expressed in the spatial arrangement of individuals, and in who does what to whom, how often, and under what circumstances. (Mason 1976: 438)

It is also useful to look at non-interactive actions of individuals in each age-sex class, to ascertain how various social and biological tasks are performed by the different members of a troop. For many species of primates, notably terrestrial forms such as macaques and

chimpanzees, long term studies of free-ranging troops have enabled researchers to perform analyses at the level of each recognizable individual. In such cases, specialized roles between and within age-sex classes have been discerned (cf. Fedigan 1976, Crook and Gartlan 1966, Reynolds 1970). We are moving towards a realization that both the variability and complexity of primate social structure are much greater than previously suspected.

In a discussion of sexual selection and sexual dimorphism in primates, Crook (1972) stated that sexual selection leads to the enhancement of behavioral and morphological characteristics that increase frequency with which males obtain mating with ovulating females. He does not explain how behavioral characteristics would be reproduced in association with morphological ones. This line of reasoning is reminiscent of a theme which persists in the literature, to the effect that a high degree of sexual dimorphism correlates directly with a high degree of differentiation between male and female behavioral profiles. The feature of sexual dimorphism which is most frequently alluded to in this vein, is the larger size and strength of adult males. These morphological differences are usually correlated with behavioral differences. Both are viewed functionally, as adaptations of terrestrial forms to predator pressure and/or strong breeding competition in which the male takes a role as 'defender' of the troop.

> As a consequence of sexual selection, therefore, many promiscuous monkeys in multimale, multifemale groups show pronounced sexual dimorphism in size, generally high levels of aggressiveness by males, and highly developed weaponry (e.g. canine teeth) in males. In general, relative to monogamous groups, there is more pronounced differentiation of roles between males and females. Males are more energetic in activities such as vigilance, leadership, and protection of the group; females are more active in direct caretaking of offspring. (Redican 1976: 355)

This statement reflects the situation in a few well-studied forms of Old World primates, macaques and baboons; and at this time merits no further application. It has given rise to a widespread impression that the role of troop 'protector' is synonymous with being a large male primate.

Smith (1973) described the concept of a 'control role' as one which included defending the troop against internal and external sources of disturbance. He states that in pigtail macaques (Macaca nemestrina) the 'control role' is superimposed on any large male in the troop who checks intragroup fighting, buffers extragroup disturbance, and acts as a focus and influence of female activities. While all these behaviors may in fact be performed by adult males in the macaque groups observed by Smith (1973), there is no justification for his suggestion that the concept of 'control role' be expanded or broadened for other primates where distribution of these tasks may be very different.

In a review of six tropical African species (all of which exhibit strong sexual dimorphism in size), Rowell (1974) noted that defense was a role feature common to

adult males. Harlow and Lauersdorf (1974) claimed that 'threat' is a masculine tendency in man and monkey, just as 'passivity' is a feminine quality with no definition of these nebulous terms. This broad generalization is based on work with caged rhesus monkeys.

In a discussion of sexual selection and dimorphism in primates, Crook (1972) details five ways that sexual dimorphism appears in primates. He says that males and females differ in:

1. Weight and muscular development
2. Body dimensions such as head and tail length
3. Pelage and markings, often in region of face
4. Particular anatomical features
5. Maturation/seasonal changes related to reproduction (Crook 1972: 238)

However, his discussion focuses on the first two of these features, as they are exhibited most strongly by baboons, to suggest that this dimorphism correlated directly with the unimale social organization and that 'predominant' male roles structure group behavior (Crook 1972: 238). Implicit in Crook's discussion is the suggestion that sexual selection inevitably produces strong sexual dimorphism in terms of male strength and size, when it is in operation within a polygynous social structure. This suggestion requires an accurate assessment of the degree to which polygyny exists, and Struhsaker (1969) points to the difficulties in defining the composition or limits of the flexible

'groups' of forest cercopithecines. Similar problems arise in a study of spider monkeys, whose flexibility in group structure defies the possibility of clearly delineating the limits of a 'group'. Sexual behavior of each individual is difficult to monitor; and without a long term study, it is impossible to ascribe individuals to 'groups'.

Another weakness in such arguments lies in their use of a hazardous assumption, first made by Darwin in his discussion of sexual selection, which implied that the 'best armed males' were also the strongest and that 'the more attractive males' were at the "same time more vigorous" (Mayr 1972: 97). Mayr pointed out that there is no necessary correlation here.

> Both Darwin and Wallace, with virtually no tangible evidence, assumed that the males which won out in a struggle with other males would mate with 'the most vigorous and best nourished females'. (Ibid: 100)

It is not surprising, then, that correlations between increased fighting ability or large size in males and a male role as troop 'defender' break down when other primate species are considered. Struhsaker (1969) criticized this presumed correlation, based on his work with forest cercopithecines. He pointed out that in drills where there is extreme sexual dimorphism in large size of males, males do not show a role as troop 'defender'. His discussion of roles in various cercopithecines emphasizes the variation between species, in terms of male and female behavioral profiles. Despite a general consistency in large and strong males in

these species, it is often the females who perform alarm calls and threaten intruders (Struhsaker 1969).

Clearly it is not safe to assume that the 'defensive' behavior comes as a package of features in adult male primates which includes greater aggressiveness, greater weapon development, higher dominance, and greater size than females. Poirier (1969) commented on the separation which exists between male and female behaviors in Presbytis entellus, a species which exhibits very little sexual dimorphism of the above type. He pointed out that males are concerned more with territorial defense toward other langur groups, while females are more alert for danger from other sources (Poirier 1969: 32). In his work with colobus monkeys where there is little sexual dimorphism in size and morphology of males and females, Marler (1969) noted the importance of male territorial displays, where both males and females participated in active defense of the troops.

Looking at sexual dimorphism of a different type, where females are larger than males and possibly heavier, Ralls (1976) considered different sorts of factors: success of a big mother or intense competition between females for some resource. It is clear that all aspects of sexual dimorphism must be investigated and compared in order to obtain realistic profiles of the complex differences which may characterize male and female primates of all ages.

Differences in Behavior Relating to Age and Sex of Nonhuman Primates

Keeping the previous discussion in mind, this section provides a review of the literature on sex differences in behavior and the development of these differences for various species of nonhuman primates. Mason (1976) suggested that the similar types of interactions within age-sex classes strengthen gregariousness and are basic to special affinities which exist both within and between classes. In most free-ranging primates individuals tend to interact preferentially with individuals of their own age-sex class, whose activities are in many ways congruent with their own (Mason 1976).

It should be added that where genealogies are known, kinship ties have proven to be fundamental in structuring networks of group interactions and overall group dynamics of the social system (Missakian 1973, Sade 1965). Such work analyzes individual behavior not only according to age and sex, but also on the basis of kinship ties and social status within the troop. Although it was not possible to ascertain the kinship ties and status of spider monkeys at Tikal, the possibility that these are active structuring devices in the local social system merits consideration.

Lancaster (1973; 1976) pointed out that the matrifocal unit, consisting of successive generations of females with their offspring (both male and female) may be an almost universal structuring principle in primate societies.

This point was also made by Gartlan (1966). It is possible that the matrifocal units described by Lancaster as structuring small foraging, resting, sleeping, grooming, and play groups of many primates, may be operative in patterning daily activities of spider monkey groups.

A pattern indicative of this female grouping has been noted in squirrel monkeys (Saimiri sciureus), where females appear to be social unifiers and males generally travel separately in hierarchically-organized groups at the periphery of a cohesive group of females, mothers, and their offspring (Coe and Rosenblum 1974). Baldwin (1968, 1969) noted that of all the interactions between various age-sex classes, those directed to adult females were the most frequent and the least aggressive; while adult males generally made few social contacts, either with other age-sex classes or among themselves. Baldwin's (1971) analysis of interactions showed strong relationships existing periodically between adult males and females, adult females and infants, and young male and female juveniles; while relations between other age-sex classes were what he called 'inconspicuous'.

Baldwin (1968) found that during mating season, adult males were generally disruptive, as they excited and frightened other members of the troop. It was also of interest that in times of general troop alarm, the adult male appeared to assume a role as investigator of the source. Baldwin cautioned that the exact nature of the role, as to what degree it benefited the troop, could not be determined.

Candland et al. (1973) felt that females were the ones most responsive to disturbances (most often the presence of a person); and that if the disturbance remained, males eventually readjusted their positions as well.

Since squirrel monkeys are arboreal New World primates dwelling in large flexible groups, it is useful to compare these findings with those from spider monkeys. The aim is not to define a 'role' for any one of these age-sex classes, as much as it is to determine conformities in behavioral configurations for males and females of each age-sex class. Indeed, Burton (1977: 11) cautioned against the use of 'role' to describe basic social tasks, or biological need-fulfilling behaviors, which might involve getting food, reproduction and rearing of young, directing group movements, protection and maintenance of group cohesion. In a survey of 21 cercopithecoid species she pointed out that these basic social tasks may be met by either sex. The organization of a particular social group is likely to have a unique distribution of tasks between the relative age-sex classes.

Looking at a few species of primates with this in mind, it becomes apparent that there is a good deal of variability in the way the tasks are distributed between the sexes, but at the same time there are some general types of consistencies which would appear to characterize the behavioral profiles of males and females. Eisenberg et al. (1972: 872) suggested that in multimale social systems, the role of the adult male usually involves the following:

1. the maintenance of group spacing with respect to neighboring troops
2. a reduction in competition by driving out younger males
3. enforcing some degree of protection against predators

As noted previously, Rowell (1974) found that captive adult males of six species of African primates retreated less than other individuals from 'attacks' made by the investigators. In keeping with this finding, Chalmers (1971) commented that certain behaviors were common to adult males of five species of Old World primates: Cercopithecus ascanius, Erythrocebus patas, Cercopithecus neglectus, Cercocebus albigena, and Papio cynocephalus (P. anubis). He said that males generally received less grooming and aggression than did adult females (Chalmers 1973: 96). Such a pattern; more directed aggression by males than females, is substantiated by Struhsaker (1969), in his observations of Cercopithecus monkeys in which adult males lead intergroup agonistic encounters and displays. However, it is of importance to note that adult females also perform alarm calls and retreat responses, which Struhsaker (1969) distinguishes from the loud display calls given by adult males which maintain group cohesion and intergroup spacing. Mason's (1960) observations of captive male and female macaques show that females respond with more fear grimaces and threats than do males to novel stimuli. This finding is in direct contrast to the broad conclusions made by Harlow and Lauerdorf (1974) that female primates

(rhesus monkeys specifically) early develop a generally passive nature.

This distinction between male displays and generalized 'aggression' which is thought to color male behaviors in general, warrants attention when behavioral profiles of adult male and female spider monkeys are discussed. Working with Nilgiri langurs (Presbytis johnii), Poirier (1969) described male displays and intergroup encounters similar to those described by Chalmers (1971) and Struhsaker (1969). Marler (1969) provided a picture of typical male territorial displays in colobus monkeys in Uganda which involves roaring, rapid and vigorous leaping, and branch-shaking. He also pointed out that this display has analogues in other arboreal primates such as Hylobates lar, Callicebus moloch, and Alouatta palliata (Marler 1969). It is noteworthy that all of these species have quite different forms of social organization. Despite the fact that there seems to be a general pattern of male 'aggressiveness', the specific context, and results of these displays show a good deal of variation.

Poirier (1969) pointed out that in langur displays, the antagonism between the participating adult males rarely involved physical contact. The chasing, and commotion of the vocal and visual antics of the males performing a territorial display need not correlate with a motivational state relating directly to 'agonism' or 'aggression'. These displays which appear territorial in function need not

correlate with protection of the troop. Poirier (1969) noted that in langurs the displays of adult males to other males were directed at outside males who were not seen to be aggressive towards young or females of the opposing groups. It is possible that displays performed by different members of the spider monkey population at Tikal may be different in nature and function.

In a study of Cercopithecus aethiops in Uganda, Gartlan (1968) defined discrete behavioral profiles for adult and juvenile males and females by analyzing their respective participation in seven categories of behavior: territorial displays, social vigilance, receiving and making friendly approaches, territorial chasing, punishing, and leading. Adult male behavior included 'punishing' and 'intergroup aggression', exclusive of other age-sex classes. However, adult males shared social vigilance activities with adult females. Most of the territorial displays and chasing were performed by adult males, although juvenile males also participated in these to a lesser extent (Gartlan 1968: 107).

In an attempt to delineate male 'roles' in primate groups with multimale social organization, Redican (1976) stated that adult males in such cases rarely performed overt 'caretaking' activities of young. Whether this generalization is warranted is a matter of some controversy given the diversity of variables involved: age of the young, relation of adult male to young, size of group and overall lack of information. In addition, occasional male adoption of

young is reported in several species of macaques (Fedigan, Zeller, personal communication).

In a very broad review of sex differences in nonhuman primate grooming, Mitchell and Tokunaga (1976) pointed out that despite great variation in grooming habits and frequencies between troops, it is generally true that adult females groom more than do males. They suggest that sex differences in grooming are more pronounced in species where sexual dimorphism is greatest. New World forms such as Alouatta and many Old World species discussed in the preceding section on sexual dimorphism would be included in this category.

In a review of solitary male Japanese macaques, Nishida (1966) noted the tendency for some adult males to move into the core of a multimale troop. Others, however, form cohesive peripheral units of two or three monkeys that may be hierarchically organized, and that are usually bonded by social or kin ties to each other. Simonds discovered the existence of a core of high-ranking males in a troop of bonnet macaques, whose grooming activities with each other clearly showed how cohesive the male network of relationships was (Simonds 1974).

In a discussion of free-ranging rhesus monkeys, Drickamer and Vessey (1973) pointed out that independence of young males from their natal group resulted in the formation of all-male peripheral groups. This peripheral association appeared to these authors to be a means of avoiding attacks

and remaining less conspicuous while young males were establishing firm ties with new group members (Drickamer and Vessey 1973: 365). Male group changing in macaques has been seen as a means of preventing incest and changing sex ratios, especially during mating seasons.

The relevance of these data to spider monkeys remains to be shown since spider monkey 'groups' and kin lines in feral populations are not easily defined, and also because there is no breeding season. However, the early independence of males from natal groups and the appearance of all-male networks in the form of independently moving units, merit consideration in a discussion of the adaptive significance of spider monkey social organization.

It seems clear that behavior of adult males is much more variable than has been generally accepted in the past. In this study where only a few adult males could be recognized and group membership was not defined, it was not possible to test for variation in adult male behavior within the age-sex class. However it is possible to test whether some of the previously discussed patterns of male behavior are substantiated in this study of Ateles geoffroyi at Tikal.

It is possible that the flexibility revealed in the behavioral repertoire of adult males may be paralleled in the behavioral profiles of adult females as well. Not only is it probable that the tasks performed by adult females vary between species and groups, but differing degrees of separation between male and female behaviors should be

expected as well.

In much of the literature there is a tendency to depict the role of the adult female strictly in terms of behaviors associated with infant-rearing. Thus qualities of maternal behavior are often projected onto all female activities. Baldwin (1969) stated that even during sexual encounters with adult males, adult female squirrel monkeys did little more than remain passive, both in consorting and copulation. He stated that this 'passive' state is induced by hormonal factors.

Mayr (1972) pointed out that female primates are more discriminating than males in choosing a male sexual partner; and that female choice is the basis of Darwin's theory of sexual selection. Because males are more obvious in many of their displays, which attract the attention not only of the females, but also of the researchers, it seems that less attention has been paid, and consequently less import has been attached to female activities other than infant care.

A general pattern which characterized most multimale-multifemale groups of primates is that of adult females forming cohesive groups with their successive generations of offspring, both infant and juvenile (Gartlan 1966, Lancaster 1973; 1976). Baldwin's (1968; 1971) observations of free-ranging squirrel monkeys indicated that adult females were responsible for the troop's unity because other age-sex classes were strongly attached to them and therefore

initiated many interactions with them. Based on her work with langurs (Presbytis entellus), Jay (1963) concluded that the behavior of adult females changes with the reproductive cycle. However, she said that adult females formed a central core of the troop at all times, while infants and juveniles moved off to play all around them.

Various categories of interactions have been used to measure affinitive bonds between and within age-sex classes of primates. Koyama's (1973) study of social bonding within bonnet macaque society (Macaca radiata), is based on the premise that the relative frequency of certain interactions which he denotes as 'dominance', 'clasped-sleeping', and 'grooming' were keys to understanding degrees of positive and negative social bonds among the various individuals. He found that adult females were the major groomers and groomees. His conclusion was that individuals of the same sex were more tolerant of each other, with the exception of mothers and male infants. This observation was based on the assumption that tolerance could be measured by the amount of clasped-sleeping he observed between male and female classes (Koyama 1973).

Simonds (1974) found similar clustering in groups of bonnet macaques, where mothers and adult daughters or other offspring groomed, moved, and sat together. He noted that there were preferences for grooming similar-sexed partners, indicative of stronger social bonds within female and male groups. Although this observation does not

preclude the occurrence of a good deal of grooming between non-related members of different age-sex classes, the prevalence of female grooming in macaques is said to be a good indication of the limits and structure of the troop (Missakian 1973). In accordance with this observation, Sade (1965) stated that since grooming is the most frequent form of overt social interaction in macaques, it is best suited for demonstrating relations between animals of different age-sex classes. He said that the amount of time spent grooming is proportional to the frequency of grooming and can be used to measure the strengths of relations. In many baboons it is noted that the females groom for longer periods, but no more often than males (Bernstein, cited in Mitchell and Tokunaga 1976: 340). Thus variations occur not only in the frequency of interactions between individuals, but also in the context and duration of these interactions.

Mitchell and Tokunaga generalize to say that these sorts of differences in grooming are indicative of overall differences in male and female socialness. They say that females are more prone to those activities involving close affinitive interactions (Mitchell and Tokunaga 1976: 342). Such a general statement illustrates the types of ideas which presently shape our perception of primate social behavior, and will be focal in the comparative study of male and female spider monkey behavior.

Development of Sex Differences

Gartlan (1968) stated that in analysis of roles for individuals of different ages and sexes, we should expect to find juveniles of one sex performing similar actions as adults of that sex, but less frequently. Differences in the behavioral profiles of adult males and females frequently involve different emphases in their relationships with other age-sex classes. The development of sex differences in young monkeys is shaped to a great extent by their associations and interactions with adult males and females.

Simonds (1974) noted that after the first two months of life, the infant bonnet macaque moves into a period of increasing sex role differentiation, dependent not only on mother-infant relations, but also on a developing network of social relationships. He found that the infant male turned to rough play groups, while infant females interacted and associated more with other females and mothers. Differences in grooming relations between mothers with male, and mothers with female infants are thought to be strong mechanisms in, and indications of, this sexual differentiation in rhesus and bonnet macaques (Sade 1965, Simonds 1974).

Jensen et al. (1967) found that with pigtail macaques (Macaca nemestrina), greater and earlier independence of male offspring was to great extent a result of the influential role of the mother, who encouraged this behavior. They noted that mothers carried female infants more than male infants, promoting longer and closer association with

females than with males.

Baldwin (1969, 1971) showed that development of sex differences seen in adult squirrel monkeys could be traced through late infancy and the juvenile period. He looked at relations among juveniles in play and found that these relations fostered dominance structures among young males. The roughness of the play excluded young females, who withdrew and engaged in more interactions with adult females and infants with whom they were seen to rest, forage, and travel (Baldwin 1969, 1971).

The relative roles of mothers, adult males and females, and peers as socializing agents of young monkeys merit consideration. These are highly dependent on associations and interactions observed between young monkeys and these other age-sex classes. In some baboon groups the high frequency of interactions between infant males and adult males indicates the importance of adult males in the development of normal sexual roles in young males (Rowell et al. 1968, Young and Hankins 1977, Ransom and Ransom 1971). The associations of infants are shaped primarily by the association patterns of adults on whom they depend. It follows that the development of sex differences in young monkeys must be considered in the social context (i.e., social system) in which they occur.

Social Organization of Ateles geoffroyi and Related Species

Feral Ateles populations have been studied in Panama, (A. geoffroyi kuhl - Carpenter 1935); in the Chiapas highlands of southern Mexico (A. geoffroyi - Wagner 1956, Eisengerg and Kuehn 1966); in Costa Rica (Freese 1976), in Tikal at the study site of this project (A. geoffroyi yucatanensis - Coelho et al. In press, Quick 1974; Coelho 1977; Bramblett 1976; Cant 1976); and in Colombia by Lewis and Dorothy Klein (Klein 1972, 1974; Klein and Klein 1973, 1976). The latter performed the most extensive study to date, studying the free-ranging population of Ateles belzebuth at La Macarena, Colombia, for eighteen months.

Other reports have been made on the small introduced group of spider monkeys, A. geoffroyi, on Barro Colorado Island (Eisenberg and Kuehn 1966, Richard 1970, Mittermeier and Fleagle 1976, Eisenberg 1976). In addition several observational projects focus on Ateles groups in zoological gardens (Eisenberg and Kuehn 1966, Klein and Klein 1971, Rondinelli and Klein 1975). Eisenberg (1976) integrates data collected from a small group of captive A. fusciceps at the National Zoological Park in Washington, D.C. with those from a study of free-ranging A. geoffroyi on Barro Colorado Island to draw some generalizations regarding behavior patterns of the genus Ateles. His focus on communicative mechanisms and integration of social behaviors is particularly important since he raises questions and makes suggestions regarding male and female roles and affinitive patterns in

Ateles. Both of these problems are focal in this project.

Although there is a good deal of controversy about the nature of a 'typical' form of social organization for Ateles, field studies have provided a working description of general patterns. Localized populations or 'troops', consisting of from 30-70 individuals, form highly mobile and fluid subgroups. Given this fluidity in associative patterns, it would be arbitrary to define 'groups' of spider monkeys. Coelho et al. (1976) did not label subunits of spider monkeys as 'groups' since they felt that observers were unable to assess the limits of groups. While they made 700 observations of social subunit compositions, they stated:

> These data do not provide an efficient means of discerning what makes up a spider monkey troop or group and how it differs from the population as a whole. . . Attempts at ascertaining the exact size and composition of spider monkey troops are thwarted by a number of factors, including:
> 1. social unit dispersion over large areas (greater than 1 km.)
> 2. social unit fission
> 3. inability of observers to recognize individual spider monkeys. (Coelho et al. 1976)

Subunits disperse within a large area for sleeping, feeding, and general movements (Carpenter 1935, Klein 1972, Coelho et al. 1974, Cant 1976, Freese 1976). Carpenter (1935) was the first to note the variability which is now known to characterize the composition and size of subgroups. He observed large multimale-multifemale groups of up to seventeen monkeys, unisex male groups from three to ten

individuals, and similar sized units of females with young. Klein (1972) supported these findings on variability in group size in his observations of 100 combinations of adult males, adult females, juveniles, and infants. While these associations appeared to change frequently, Klein computed the mean subgroup size during eleven months of observations in Colombia to be 3.5 individuals. This number approximates Freese's estimate of average subgroup size for Ateles in Costa Rica (Freese 1976). At Tikal both Bramblett's team (1976) and Cant (1976) identified similar patterns in Ateles social organization. They distinguish large troops of up to seventy individuals of all ages and sexes. These troops fraction into smaller groups which maintain a certain cohesiveness and communication both within and between groups during their daily activities.

Coelho et. al. (1976) noted that subunits range in size from 1-75 animals, but that 74% of all subunits contained 1, 2, or 3 monkeys. They also described that spider monkeys make circular migrations each day. They report that there are daily circular migrations of monkey groups. Parties of monkeys leave one of the favored sleeping sites, travel throughout the local habitat, and return to the sleeping sites, reuniting as a larger association at night. Two forms of migrating units were involved: non-fragmenting and fragmenting social units. The former consisted of all age-sex categories which maintain their size and composition (reportedly up to 70 monkeys) through the day, shifting

rapidly from compact to dispersed association. Coelho et al. (1976) distinguished these groups from fragmenting subunits of about ten individuals of mixed age-sex classes, but point out that these in turn fission into smaller less heterogeneous units; i.e., all adult male, adult female, adult female and juvenile, female with juvenile and infant, or female with infant (Coelho et al. 1976).

Despite the fact that discussion of Ateles social organization has focused on the flexibility of groups, certain consistencies in social relationships and internal structuring of groups do appear across populations. Although there is fluidity in the social organization, stable sets of socialization processes produce consistency in behaviors of individuals of different sexes (Rondinelli and Klein 1975). The resultant differences in behavioral profiles are reflected by the sexual segregation which has been reported in Ateles grouping patterns.

It is generally agreed that spider monkeys show non-random association tendencies, based on divisions of age and sex (Klein and Klein 1971, Klein 1972, Rondinelli and Klein 1975, Eisenberg 1976, Cant 1976). Analyses of associative tendencies and grouping in both captive Ateles belzebuth in San Francisco and feral monkeys in Colombia revealed that males tend to form age-graded subunits (Rondinelli and Klein 1975). These age-graded subunits are independent in their movements with respect to the rest of the troop; that is, associations of females with

juveniles and/or dependent infants. (Adult males frequently move in and out of these associations as well). Eisenberg and Kuehn (1966) suggested that social rank order accounted for the differences in interactions between individuals more than did other criteria, such as sex. However, in a later publication, Eisenberg (1976) looked at age and sex to account for observed behavioral distinctions and grouping patterns in Ateles geoffroyi.

Lancaster (1976) indicated that dominance as it is understood in well-studied macaque and baboon troops plays a much smaller role in structuring groups of arboreal primates. Cant (1976) pointed out that there is a low degree of dominance structuring in the relations between males in spider monkeys. He said that the minimal sexual dimorphism in size and morphology in male and female spider monkeys could not be correlated with a reduction in male-male competition in the groups he studied at Tikal. Crook (1972) suggested that a lack of sexual dimorphism in size should be correlated with a reduction in male dominance from terrestrial unimale groups of primates.

Thus it is necessary to look at other structuring principles in the interactions between and within age-sex groups. Referring to primates in general, Eisenberg et al. (1972) pointed out that male unisexual associations, like those of females, are age-graded groups strongly reflecting kinship ties:

> ... mutual tolerance among males has an orderly developmental succession based on continually renewed contact over many years. (Cited in Eisenberg 1976: 3)

Despite the noteworthy fluidity of Ateles social organization, it is possible that stable sets of socialization processes permit strong bonds to develop and be maintained between males.

Strong affiliations characterize the associations and interactions between females and offspring, and large juvenile males associate very little with these female associations (Cant 1976). Cant also noted that females with offspring of similar ages often congregated in groups, enabling juveniles and infants to play with other individuals of their own ages and sexes (Cant 1976). He felt that young males showed earlier independence from the female associations than did their female peers, by their frequent interactions with adult males.

Eisenberg (1976: 3) stated that the male subgroupings cooperated in offensive and defensive interactions. Cant (1976) noted that most of the agonism within localized groups was that of males chasing females. Klein (1974) also commented on the high frequency with which males directed agonism at adult females in feral populations of Ateles belzebuth. Male parties also engaged in what Cant (1976) termed 'long distance agonistic behavior', and Klein (1974) denoted as 'confrontation' behavior. Both authors speculated that these are forms of territorial displays. In addition, both free-ranging and captive adult male spider monkeys may

perform threat behaviors and initiate long calls more than do other individuals (Eisenberg 1976).

Adult females on the other hand, tend to associate with female partners, but Cant (1976) stated that they were more 'solitary' than he predicted. It was noted that females with infants of a certain age were more likely to associate with other females with like infants (Cant 1976). Eisenberg (1976) suggested that the strong bonds between females and young are revealed by looking at the attendant grooming relationships between them.

The Study Species: Distribution and Description of Ateles geoffroyi and Related Species

Spider monkeys (genus Ateles) are arboreal primates belonging to the family Cebidae. Although exact distributional limits are poorly defined, it is thought that Ateles inhabits neo-tropical forests as far north as the Mexican state of Tamaulipas and as far south as 16° S in Bolivia (Klein 1972: 114). In general, spider monkeys frequent forests at altitudes of about 800 meters, but they range from sea level up to about 2500 meters in Colombia (Hernandez-Camacho and Cooper 1976).

It is generally accepted that the genus Ateles can be divided into 4 species and sixteen sub-species (Kellogg and Goldman 1944). Because of the paucity of literature on each of these species: Ateles paniscus, A. belzebuth, A. fusciseps, A. geoffroyi, behavioral differences attributable

to taxonomic separation are unknown. Although Napier and Napier (1967) recognize this categorization, Klein (1972) suggested that the four species might be re-classified as A. paniscus; and that the genus Ateles be expanded to include woolly spider monkeys (Brachyteles arachnoides).

Spider monkeys are diurnal primates although some social interaction and movement do occur at night, especially during nights with moonlight (Eisenberg 1976, Cant 1976). Structurally, spider monkeys are well adapted to their highly mobile lives in the canopies of tropical forests. They exhibit a locomotor pattern which has been termed semi-brachiation (Napier and Napier 1967: 62) because of their use of a fifth limb (tail) to aid their brachiating style of movement. Recent work by Cant (1976) in Tikal reveals how versatile their locomotor habits are, including almost all combinations of leaping, branch running, and walking. A prehensile tail with a dermatoglyphic pad, loss of thumb giving the hand a hook-like grasp, trunk shortening and a specialized flexible scapula; all provide the spider monkey with unique hand-over-hand suspended progress through the trees, with a tail support during this vertical carriage (Erikson 1963). In any event, the variety of movements of which spider monkeys are capable, makes their rapid travel through the discontinuous canopies of the forests possible.

Spider monkeys are the second largest of all New World primate genera, surpassed in size only by Lagothrix. They range in size (head and body length) from 37-59 cm for

males (Napier and Napier 1967: 59). Eisenberg (1976) noted that these data represented samples in which the true ages of the specimens were not known. Since the males are often caught in association with adult females, it seems likely that many of those measured may have been sub-adult males. The weight of subadult males (A. fusciceps) starts to surpass that of adult females at 36 months, and Eisenberg (1976) suggested that adult males are indeed larger and slightly heavier than adult females. From observations at Tikal, I had the strong impression that this differentiation was true for the Ateles geoffroyi population there. This suggestion concurs with Cant's (1976) observations, that the adult males were larger, in that they were more robust than adult females at Tikal (Cant 1976). Klein, however, found that females were 3-4% heavier and larger than males in a population of A. belzebuth in Colombia (Klein 1972).

Spider monkeys are primarily frugivorous. Carpenter (1935) speculated that the spider monkey social system with its seeming ability to generate groups of almost any size and composition, is adapted to seasonal variations in the occurrence and availability of fruit in trees. Similarly Durham (1971) suggested that variation in group size and composition of spider monkeys at different altitudes in Peru reflected differences in fruit trees at these altitudes. Freese (1976) noted that marked seasonality and lack of uniformity in fruit trees were both factors in the flexibility of spider monkey behavioral patterns in Costa Rica.

Klein (1972) detailed three characteristics of social variability which he could easily quantify: subgroup size, subgroup dispersion, and subgroup composition in terms of age-sex status of its members. He then correlated these with qualitative data on fruiting trees: local distribution, length of fruiting season, and the qualities of the fruit which might affect behaviors involved with eating them. These include fruit size, its accessibility, and nutritional value.

Klein (1972) noted that grouping patterns fluctuated consistently with fruiting periods of the various trees. He also observed a consistent spatial orientation of individuals feeding within a free, in that individuals maintained a constant minimum distance from each other, regardless of fruit dispersion or clustering within a tree. Such spacing seems dependent on certain ritualized mechanisms and specialized greeting gestures and communication signals. Klein (1972) said that the pectoral sniff and embrace appeared to be a fundamental device in the regulation of group dispersion within a tree, as it was used by adult males leaving and coming into a tree. In addition it seems likely that chemical communication may play an important role in this spacing (Klein 1972).

Spider monkeys have a large concentration of apocrine glands at the cranial edge of their sternum, which appear to function in scent-marking of trees (Klein and Klein 1971; Klein 1972). As well the hypertrophied clitoris of

the females is used frequently for urine-marking tree branches (Klein 1972). Both the frequency of female place-marking and male place-sniffing are indicative of the use of olfaction in spider monkey communication (Klein 1972).

Because there is no evidence for a distinct mating season in spider monkeys, variation in behavior of males and females attributable to sexual activity is difficult to determine. This situation is in direct contrast to Saimiri species, in which the males become heavily fatted and interact much more with females during mating season.

CHAPTER THREE

METHODS

The Study Area and the Study Group

The study site for this project is located in the southeast corner of Tikal National Park, a 576 km^2 area under the jurisdiction of Dr. Luis Lujan, Director of the National Institute of Anthropology and History in Guatemala. Tikal was once the largest ceremonial city of Mayan civilization, and it was abandoned around 900 A.D., as was the rest of the Peten at this time (Lundell 1937). Spider monkey motifs in Mayan art suggest that these primates probably have inhabited this region since as early as 0 A.D.

The entire region surrounding the park, the northern Petén of Guatemala, is covered by quasi-rainforest (Lundell 1937). The year is clearly divided into dry and wet seasons, which last from about November to May and May through October, respectively.

The vegetation at Tikal is characterized by a ramonal association, with a preponderance of ramon trees, Brosimum alicastrum. The zapote or sapodilla (Achras zapota) is thought also to owe its predominance to Maya horticulture, and/or its success in areas with limestone mounds, which are so concentrated in this archaeological site (Lundell 1937). Fruits of both these trees form a major part of the diets of the spider monkeys at Tikal.

The study site offers many advantages for the study of Ateles social behavior, which requires long contact

periods with the monkeys. Archaeological work in the area dates back to 1881; and since 1956 the University of Pennsylvania has been carrying out extensive excavation, which included mapping and surveying the area. Therefore a very detailed and extensive map of greater Tikal is available; a map which shows the ruins, and physical features which facilitate orientation of the researchers (Carr and Hazard 1961).

Tikal has also been the site of other primate study projects, which provide basic information about the daily activity patterns of the monkeys there (Bramblett 1976, Coelho et al. 1974, Quick 1974, Cant 1976).

The study population at Tikal has been identified as Ateles geoffroyi yucatanensis, although some variation in pelage makes some individuals reminiscent of neighboring sub-species, A. geoffroyi villerosus (Quick 1974: 6). The local population size in 1972 was estimated to be about 225 individuals who base their activities within a 5 km^2 area, with a resultant density of about 45 animals per km^2 (Coelho et al. 1974: 5). Cant, however, reported that the density was much lower than this figure during his work in 1976. His estimate, based on exhaustive censusing of the local population, was 28 animals (monkeys) per km^2 (1976). He estimated that the population was 50% adult, that juveniles accounted for 37%, and that infants comprised 12% (Cant 1976). My preliminary study carried out in May of 1977, and the field study conducted during the winter of 1978, indicated that at these times the population size was

much closer to Cant's estimate.

The local primates, A. geoffroyi and Alouatta villosa pigra, are not provisioned in any way, nor do they interact at all with the people in the area. Tikal is a National Park, and an archaeological site which has been excavated for the past 20 years; and thus the primates are fairly well-habituated to human presence without being adversely affected by it. It cannot be overstressed how much the habituation of these protected monkeys facilitated data collection. In areas outside of the central park, where poaching seems to persist, it is almost impossible to maintain visual contact with spider monkeys for more than a few seconds, due to their obvious fear of human presence.

A preliminary survey of the site of Tikal and its primate population was undertaken during the month of May 1977. At this time it was possible to become thoroughly familiarized with both the layout of the study area and the daily activity patterns of the spider monkeys. Observation techniques were practiced, data sheets and sampling procedures were standardized, and a tentative ethogram was compiled at this time.

Collection of Data

Data collection was begun in January of 1978, when the author returned to Tikal accompanied by a field assistant to aid in the recording of data. Between the

months of January and May of 1978, a total of 550 hours were spent in the field, either locating or observing monkeys. The researchers were actually in visual and/or auditory contact with monkeys for 319 hours, and a total of 150 hours of quantitative behavioral data were collected.

Data were recorded mostly within a 25 km^2 area, encompassing both the central part of the archaeological site and the surrounding area in which one localized population of Ateles geoffroyi ranged. This area was bordered on one side by the road into Tikal (which provided no arboreal crossing points for the monkeys), and seemed to extend as far north as the road leading to Uaxactun. Because the site is criss-crossed by transects extending 10 km in the four cardinal directions, the researchers were able to follow monkeys through dense jungle by maintaining a compass bearing, and then return via these cleared swaths, gauging distances covered from the central area.

Initially attempts were made to sample individuals in what were apparently neighboring populations of Ateles geoffroyi to that one inhabiting the central area. However, individuals in a separate population on the south side of the Remate Road leading to the park were extremely excitable in the presence of human observers, probably because of the adverse effects of poachers in the less guarded outskirts of the central area. Hence it was virtually impossible to collect data on social behavior in troops outside the central 25 km^2, where the monkeys were well protected and habituated to human presence.

Given the free-ranging nature and flexible grouping patterns of these arboreal monkeys, positive identification of all individuals was not possible in the five months of the study. By the end of this time, about ten individuals were positively identified by various distinguishing marks. One adult male had a large stomach tumor, another had a stump tail, one adult female had a crippled and immobilized right leg, while an adult male was clearly identified by his severely injured right arm. Many more were becoming familiar to the researchers at the end of the study, by their appearances and associative patterns with other distinctive monkeys.

For the purposes of data collection, however, the researchers identified individuals only by age and sex. Seven categories were recognized in this study: adult male, adult female, juvenile male, juvenile female, infant male, infant female, and mother with infant.

Cant (1976) used age grades devised by Eisenberg (1976) for his work at Tikal. Infants are distinguished from juveniles by their dependence on mothers who carry infants and not juveniles during times of rapid progression through the trees. This definition is used in this study to distinguish infants from juveniles. Based on size estimates and behavioral indicators, Cant (1976) also distinguished three age grades for juveniles:

Juvenile 1 -estimated age in months: 12-20
Juvenile 2 -estimated age in months: 20-36
Juvenile 3 -estimated age in months: 36-48 (Males)
36-56 (Females)

Cant stated that when ambiguity arose in assigning an individual to one of these categories, it was usually in deciding whether males were Juvenile 3 or adult. He used associative patterns of the individual in question to make the classification. Thus he felt that social and physical attributes could be used to characterize the stages of juvenile development, and that because females met these criteria for 'adult' at an earlier age, slightly more adult females than males, and more juvenile males than females were present (Cant 1976).

This study analyzed behaviors assigned to broad age classes of adult, juvenile, and infant. A young monkey was termed infant if it was seen being carried at any time by its mother. This categorization often required that the researchers wait several minutes after the session was completed, until the monkeys moved off, to make this decision. For categorizing individuals as juveniles and adults, physical characteristics were assessed. Thus adult monkeys were those with fully developed genitalia, distinguishable by their size, coloration, hair covering in males, and overall appearance. This category includes what Cant called Juvenile 3, or subadult males and females, and adults (Cant 1976). After extensive censusing of the population of Ateles geoffroyi at Tikal, Cant's impression was that when they were combined, the Juvenile 3 and adult classes had nearly equal numbers of males and females.

Juvenile monkeys in this study correspond to those

deemed Juvenile 1 and Juvenile 2 by Cant (1976), ranging from about 12-36 months in age. Thus any individual independent from its mother for locomotion, but not showing physical maturity, was classified as juvenile. Cant (1976) found that the sex ratio within this category was almost equal.

A day of data collection began when the researchers encountered one or more monkeys, typically by returning at dawn to the area in which monkeys had last been seen the previous dusk. At dawn the loud howling calls could be heard throughout the central area, apparently assisting the monkeys (and the researchers) in determining the locations of, and pathways in use by other monkeys. Once one or more monkeys were located, data collection commenced.

Focal animal sampling was used primarily as a means of ensuring that a cross-section of age-sex classes, and the interactions between and within these classes, was obtained. Focal animal subjects were chosen for each data session on the basis of their observability and proximity to the researchers. However, a conscious effort was made to sample individuals of all ages and sexes, in various contexts and at varying times of the day, in order to compensate for the biases inherent in opportunistic sampling.

The same subject animal was not chosen (knowingly) for two consecutive sessions. If all individuals in an isolated unit had been chosen once as focal animals, quantitative data collection ceased and only qualitative

notes were made until such time as the group reunited with other monkeys, or moved to a new area and changed its basic activity and spatial patterns. For example, each of three monkeys foraging together in a zapote tree would be sampled only once, until such time as they were joined by another unit, or perhaps began to clump together in a new sequence of behaviors such as grooming or resting. At this point the researchers would resume taking quantitative data. This procedure ensured that the behaviors of individuals performing very obvious displays or easily observed interactions (such as sleeping together) did not receive undue attention.

Data were recorded on data sheets (Appendix 1) by the field assistant, who wrote down the observations as they were verbalized by the observer watching the monkeys. Each data sheet represents a 5 minute (300 second) interval, during which the behaviors of a focal animal were observed and recorded. Focal animal data were used only if the subject were visible to the observer for the entire five minute period. Longer sessions would too often have been impossible to complete given the rapid transitions in activities and locomotion of spider monkeys, while good cross-sections of these activities could usually be obtained in five minutes.

In addition to these quantitative data, continuous qualitative data in the form of descriptive field notes were made. Group movements were plotted and notes made of

the types of food sources being utilized, group compositions, spatial orientation of individuals, and any other sorts of information of note to the observers. For instance, continuous notes were made during incidents such as sexual behavior, displays, or interspecific encounters. Records of precipitation and temperatures were also kept.

Each time period provided a variable number of behaviors and interactions with other individuals. The date, time, and location were all recorded at the start of each time session. A note of all monkeys sighted by the researchers during the five minute interval and a brief description of the general context of the activities was made for the purposes of reference to specific events. For each action performed, or interactions engaged in by the focal animal during the five minute interval, the following information was recorded: the time in seconds at which it began, the action occurring, whether the focal animal was the recipient or initiator of the behavior (if it was an interaction), and the age-sex class of the other participant if there was one involved. Descriptive comments were also made about each action, if they added context to the quantitative data.

Although <u>actions</u> of one individual subject were recorded during each 300 second interval, the <u>interactions</u> between that subject and other monkeys were also of importance. Given Cant's (1976) findings that there were fairly equal sex ratios in both juvenile and adult classes, and

the fact that an attempt was made to choose approximately equivalent numbers of male and female animals of each age-sex class, it was felt that some degree of control was maintained over possible biases incurred by opportunistic sampling of individuals and their interactions with others. In all, 570 adult males, 507 adult females, 168 juvenile males, 220 juvenile females, 105 infant males, 134 infant females, and 89 mothers with infants were selected through focal animal sampling.

For the purposes of data collection, 51 actions were defined based on both preliminary observations at Tikal and additions which were made as new actions were observed during the five months of study in 1978. These are listed and described in the ethogram (Appendix 2). Included in this list are all types of activities in which spider monkeys were seen to engage. Not all were analyzed here since their diversity in form and function meant that many did not illuminate social relationships, or differences in behavioral profiles between ages and sexes (i.e. finger sniff, spar).

Analysis of Data

Because of the diversity of the actions listed in the ethogram, it is impossible to classify all of them according to either form or function. However, some broad classes of behaviors are used here for clarification of analyses and results.

Some actions involve basic biological tasks or bodily functions necessary for immediate survival of the individuals. These functions include eat, drink, urinate, defecate; and they do not illuminate sex differences in social relations or behavior. These behaviors require no other participant, and are tabulated as Non-interactive behaviors (Table I).

Included in non-interactive behaviors are 'self-directed' and 'no-object' actions. Locomote, sit, chest rub, branch rub, scratch, look around, finger sniff, branch sniff, break contact, groom, genital touch, and touch can be classified as Non-interactive behaviors. Because the meaning of each is so highly dependent on its context, it was not fruitful to analyze these behaviors separately. However, certain motor patterns or actions such as 'look around', 'branch shake', 'display howl', 'contact call', and 'pectoral sniff and embrace' were more easily interpreted. Their frequency of occurrence in each age-sex class was tabulated.

Still other actions occurred very infrequently, or were limited to one age-sex class and did not warrant quantitative or comparative analysis. Erection is such a behavior, seen only in males, and often difficult to monitor.

The actions which involved interactions were the focus of much of this analysis, since their occurrence between and within age-sex classes reflected social relationships. For the purpose of analyses some interactions

were grouped qualitatively as 'affinitive', 'agonistic', or 'play'. Behaviors are categorized this way on the basis of simple working definitions. Affinitive interactions include 'groom', 'approach', 'embrace', 'touch', 'follow', and 'solicit groom', all of which reduce or maintain proximity of monkeys with each other. Although 'sit in contact' and 'sit beside' are also affinitive by definition, they were analyzed in a separate table because their duration was considered to be of a greater significance than direction or frequency (Table III). 'Groom' was included in affinitive interactions, but was also analyzed separately for frequency and durations of bouts between and within age-sex classes. This procedure was followed in order to compare spider monkeys with many Old World species for whom grooming is said to be the most important activity for promoting and maintaining social bonds (Sade 1965, Missakian 1973).

Agonistic interactions were so defined because they served to increase distances between individuals, and generally involve some form of threat or symptoms of distress. Behaviors which conform to Klein's (1974) altercations and supplantations, and Cant's (1976) short distance agonism, are included in this tabulation of agonistic encounters: 'chase', 'attack', 'displace', 'being retreated from'. Other forms of interactions are analyzed separately because of differences in their occurrence and context.

'Branch shake' is treated independently because it was seen most frequently as a threat directed towards

human observers. It was not recorded as such when it was a part of a sequence termed the 'display-howl' which corresponds with Klein's (1974) confrontation behavior and Cant's (1976) long-distance agonism between groups of monkeys.

Special note was paid to the interactions and relationships between mothers and infant males and females. The times that mothers spent carrying, eating in contact (with infant on their backs), bridging for, and sitting with infant females are compared to those for infant males. Given the elongaged clitoris of the infant females it was generally easier to sex them than it was to sex infant males, especially when the infants were being carried by their mothers (either ventrally or dorsally). Thus more infant females with mothers were sampled than were infant males and mothers. It was therefore not possible to ascertain the exact significance of the differences found between infant female and infant male care by mothers.

Other categories of behavior which were analyzed include 'play' and 'vocalization'. Both of these involve combining actions described in the ethogram, because researchers were unable to differentiate between gradation of these individual actions. 'Play chase', 'grapple', and 'play' are all analyzed for duration under 'play'. The play vocalization usually accompanied 'play', and was used to distinguish it at the time of recording; but was not analyzed separately. 'Vocalization' includes 'grunt', 'growl', 'whine', 'barks', and 'vocalize'; and the frequencies

of these are tabulated. In addition three copulations are described.

Presentation of Data

This study focuses on two major issues which shaped the analysis of data and discussion of results. Firstly, it is concerned with social interactions between and within age-sex classes, since these are indications of the social relationships which structure the social system. Secondly, this study is focussed on the basic behavioral profiles for each age-sex class, as they are represented by the data collected on actions (both interactions and non-interactive behaviors) for each age-sex class.

The results from analyses of different kinds of interactions between and within age-sex classes are detailed in separate tables and figures. Results from tabulation of actions (non-interactive) are presented on separate tables, showing the frequency with which they were performed by focal animals of each age-sex class. Frequencies and durations of behaviors were obtained in cross-tabulations from computer runs of SPSS (Statistical Package for the Social Sciences). Grooming is a behavior for which variation between certain ages and sexes in durations of bouts has been shown to characterize differences in relations (Mitchell and Tokunaga 1976). Thus analysis of variance tests were performed on the mean lengths of grooming bouts between and within age-sex classes. A table showing

significant results is included.

Null hypotheses of no preferences for male and female partners for various interactions were tested using computer runs of Fisher's Exact Probability (Siegel 1956). These tests were performed on two by two contingency tables for affinitive interactions, sitting together, grooming, and agonistic interactions. These contingency tables are provided, with the probabilities obtained for each.

In this study mothers with infants were treated separately, distinct from adult females, in order to separate differences attributable to biological and behavioral requirements of being a mother from those behavioral elements which might be attributable to the socialization process of adult females.

CHAPTER FOUR

RESULTS

Action Patterns

Table I shows the frequency of all non-interactive behaviors for 1793 focal animals. These behaviors are categorized into three broad classes: those performed as independent actions by the focal animal (i.e., eat); those directed by the focal animal at itself (i.e., scratch); and other interspecific interactions of the subject with local birds, animals, or human observers (i.e., branch shake). The behaviors included in each of these categories are listed at the bottom of Table I.

On the bottom of Table I, it can be seen that of all the 18,522 actions, 12,679 (58%) were of the first three types, not involving interactions with other individuals. From the relative number of focal animals sampled within each age-sex class (First column, Table I), it is evident that adult females accounted for more non-interactive behaviors than might have been expected. Adult females accounted for 28% of all focal animals sampled, but the non-interactive behaviors of adult females accounted for 33% of the total. Conversely, infants performed somewhat fewer non-interactive behaviors than expected, given the relative number of infants sampled. Infant males comprised 6% of the total sample of focal animals, but they only accounted for 3% of behaviors not involving interactions.

Table 1. Frequency of All Non-Interactive Behaviors Performed by Focal Animals in Each Age-Sex Class

		Focal Animals	No Object	Self	Other	Total
AM	Frequency	570	3563	343	163	4069
	% Total	32	33	30	23	32
AF	Frequency	507	3626	352	265	4243
	% Total	28	34	30	37	33
JM	Frequency	168	942	75	52	1069
	% Total	9	9	6	7	8
JF	Frequency	220	1198	121	80	1399
	% Total	12	11	10	11	11
IM	Frequency	105	327	76	7	410
	% Total	6	3	7	1	3
IF	Frequency	134	440	147	13	600
	% Total	8	4	13	2	5
Mo	Frequency	89	708	45	136	889
	% Total	5	6	4	19	7
	Total	1793	10804	1159	716	12679

(68.5%) 12679 Non-Interactive Behaviors (Table I)

(31.5%) 5843 Interactions (Table II)

TOTAL 18522 Actions

No Object: Eat, Locomote, Sit, Look Around, Finger Sniff, Branch Sniff, Yelp, Grunt, Vocalize, Urinate, Defecate, Drink, Agonistic Bark, Growl, Erection, Distress Bark, Whine, Branch Rub, Play Vocalize.

Self: Chest Rub, Arm Rub, Touch, Groom, Scratch, Genital Touch.

Other: Branch-Shake, Open-Mouth Threat, Display-Howl, Spar

Infant females performed only 5% of all such actions, but they accounted for 8% of the focal animals sampled.

Of the total number of actions, 5843 cases (32%) were interactions in which the focal animal was engaged in simultaneous and definite interactions with another individual. Table II details the frequencies with which each age-sex class was involved in an interaction with individuals of the seven age-sex classes. Although this table does not distinguish between these interactions in a way that shows how individuals were interacting, it does provide an indication of how much each age-sex class interacted. Except for the high frequency of interactions between mothers and infants, interactions between adult males were the most prevalent. Adult males in interaction with other adult males accounted for 40% of all interactions recorded for adult males. Interactions between males and mothers represented 52% of all infant male interactions; while those between infant females and mothers accounted for 69% of all infant females, and 45% of all mother-infant interactions.

Some preferences for interactions with same-sex partners can be discerned from Table II. Of all adult male interactions, 16% were with juvenile males and only 4% were with juvenile females. These interactions with adult males accounted for 34% of all juvenile male and 6% of all juvenile female interactions.

Interactions of adult females were relatively more evenly distributed than were those of adult males.

Table II. Frequency of Interactions Between and Within Age-Sex Classes

		AM	AF	JM	JF	IM	IF	Mo	Total
AM 32% sample	No. of Interactions	763	411	314	68	127	87	158	1928
	% of AM Interactions	40	21	16	4	7	4	8	
	% of All Interactions	13	7	5.4	1.2	2.2	1.5	2.7	34
AF 28% sample	No. of Interactions	411	347	142	476	51	39	198	1664
	% of AF Interactions	25	21	8	29	3	2	12	
	% of All Interactions	7	5.9	2.4	8.1	.9	.7	3.4	28
JM 9% sample	No. of Interactions	314	142	99	140	98	39	99	931
	No. of JM Interactions	34	15	11	15	10	4	11	
	% of All Interactions	5.4	2.4	1.7	2.4	1.7	.7	1.7	16
JF 12% sample	No. of Interactions	68	476	140	181	91	141	113	1210
	% of JF Interactions	6	39	12	15	10	4	11	
	% of All Interactions	1.2	8.1	2.4	3.1	1.5	2.4	1.9	21
IM 6% sample	No. of Interactions	127	51	98	91	39	72	511	989
	% of IM Interactions	13	5	10	9	4	7	52	
	% of All Interactions	2.2	.9	1.7	1.5	.7	1.2	8.7	17

Table II. Frequency of Interactions Between and Within Age-Sex Classes (continued)

		AM	AF	JM	JF	IM	IF	Mo	Total
IF 8% sample	No. of Interactions	87	39	39	141	72	49	930	1357
	% of IF Interactions	6	3	3	10	5	4	69	
	% of All Interactions	1.5	.7	.7	2.4	1.2	.8	16	23
Mo 5% sample	No. of Interactions	158	198	99	113	511	930	60	2069
	% of Mo Interactions	8	9	5	5	25	45	3	
	% of All Interactions	2.7	3.4	1.7	1.9	8.7	16	1.0	35

Interactions: Contact call, Follow, Approach, Retreat from, Embrace, Pectoral Sniff and embrace, Touch, Groom, Solicit groom, Play chase, Nurse, Sit in contact, Carry, Displace, Genital touch, Break contact, Grapple, Sit beside, Play, Eat in contact, Bridge, Chase, Copulate, Attack

Interactions with adult males accounted for 25% of all adult female interactions, 21% were with other adult females, 8% with juvenile males, and a high 29% were with juvenile females. Interactions with adult females represented 39% of all juvenile female interactions and 15% of those of juvenile males.

In order to determine how the interaction patterns of age-sex classes of spider monkeys differed, separate categories of qualitatively distinct interactions are examined. These categories are defined and described in the preceding methods section. Results of analyses of each of these categories are presented here.

Affinitive Interactions

The affinitive behaviors of 'carry', 'bridge', and 'eat in contact', which occur almost exclusively between mothers and infants are treated separately in a section dealing with mother-infant interactions. While frequencies of 'groom' are included in Table III, independent tabulation of these incidents was also performed, and is shown in a later section.

Table III shows the frequencies of affinitive interactions initiated and received by each age-sex class. Column percentages indicate the percentages of the total number of affinitive interactions received by each age-sex class.

The frequencies of affinitive interactions shown

Table III. Frequency of Directed Affinitive Interactions Between and Within Age-Sex Classes (Follow, Embrace, Touch, Groom, Solicit Groom, Approach)

INITIATES		RECEIVES AM	AF	JM	JF	IM	IF	Mo	Total Initiated
AM	Frequency	359	63	37	17	6	5	40	527
	% of Row	68	12	7	3	1	1	8	
32% sample	% of Column	51	12	22	6	5	4	7	
	% of Total	14	3	1.5	1	-	-	2	21
AF	Frequency	118	161	26	94	12	6	69	486
	% of Row	24	33	5	19	2	1	14	
28% sample	% of Column	16	30	15	37	10	4	12	
	% of Total	5	7	1	4	1	-	3	19.5
JM	Frequency	93	41	41	9	9	4	41	238
	% of Row	39	17	17	4	4	2	17	
9% sample	% of Column	13	8	24	4	8	3	7	
	% of Total	4	2	2	-	-	-	2	9.5
JF	Frequency	26	185	14	64	9	26	63	387
	% of Row	7	48	4	16	2	7	16	
12% sample	% of Column	4	35	8	26	8	19	11	
	% of Total	1	7	1	3	-	1	3	15.5
IM	Frequency	48	17	25	8	10	4	152	264
	% of Row	18	6	9	3	4	2	58	
6% sample	% of Column	7	3	15	3	8	3	26	
	% of Total	2	1	1	-	-	-	6	10.6
IF	Frequency	28	17	8	30	14	16	186	302
	% of Row	9	6	3	10	5	5	62	
8% sample	% of Column	4	3	5	12	12	12	33	
	% of Total	1	1	-	1	1	1	8	12.1
Mo	Frequency	37	47	20	29	57	75	26	291
	% of Row	13	16	7	10	19	26	9	
5% sample	% of Column	5	9	12	12	49	55	4	
	% of Total	1.5	2	1	1	2	3	1	11.7
Total Received		709	531	171	251	117	136	580	2495
	% Total	28.4	21.3	6.9	10.1	4.7	5.4	23.2	

on Table III indicated the possibility that preferences for partners of the same sex shape the occurrence of affinitive interactions both within and between age classes. For instance, the high frequency of interactions noted previously between adult males (Table II) is, at least in part, a reflection of the frequent affinitive interactions which occurred between adult males. Affinitive interactions between adult males accounted for 68% of all affinitive interactions initiated by adult males, and 51% of those received.

To test whether there were significant preferences for same-sex partners in affinitive interactions, the following null hypothesis was formulated:

> The choice of a partner in affinitive interactions, between and within age-sex classes, is not dependent on the sex of that partner.

Using the appropriate two by two contingency tables derived from Table III, the probabilities of the frequencies with which affinitive interactions occurred within and between age classes were obtained (Fisher's Exact Probability, Siegel 1956).

Table III(a) shows these nine contingency tables, and gives the relative probabilities of each. Significant results were obtained for the interactions between adults, between juveniles and adults, between adults and juveniles, between juveniles and infants, and between infants and juveniles. The null hypothesis was rejected in all these cases.

Table III(a). Probabilities of Occurrences of Affinitive Interactions Between and Within Age-Sex Classes (All Probabilities derived using Fisher's Exact Probability)

	AM	AF	JM	JF	IM	IF
AM	359	63	37	17	6	5
AF	118	161	26	94	12	6
	$p < .001$	n=70*	$p < .001$	n=174*	$p < .40$	n=29
JM	93	41	41	9	9	4
JF	26	185	14	64	9	26
	$p < .001$	n=345*	$p < .001$	n=128*	p=.008	n=48*
IM	48	17	25	8	10	4
IF	28	17	8	30	14	16
	p=.14	n=110	$p < .001$	n=87*	p=.11	n=162

* Hypothesis of no preference for sex of partner rejected p .151

On examination, the preferences found here were all for same-sex partners in affinitive interactions. Within the adult class, affinitive relations appeared to be the strongest between adult males; while adult females showed a somewhat weaker preference for affinitive interactions with adult females. Juvenile relationships with each other also showed a division between the sexes.

Between juveniles and adults, there appeared to be a set of mutually affinitive relationships with members of the same sex. The strongest preference appeared to characterize the affinitive behaviors directed by juvenile females towards adult females. These accounted for 48% of all affinitive interactions initiated by juvenile females, while those of juvenile females with adult males accounted for just 7% (Table III).

Similarly, juveniles and infants, in affinitive interactions with each other, showed a mutual tendency to interact with individuals of the same sex (Table III(a)). Both affinitive interactions initiated and received by juveniles, in interaction with infants, indicated that relationships between juveniles and infants are generated more with partners of the same sex than they are with members of the opposite sex.

It can be seen that except for their interactions with juveniles, infants showed no other significant preferences for affinitive interactions with male or female partners: Table III(a). Adults (excluding mothers)

appeared to maintain equivalent affinitive relationships with both male and female infants, as did infants with adults. Infants did not promote affinitive relationships preferentially with same-sexed infants.

Sex differences in primate behavior are frequently correlated with differences in the amount of agonistic and affinitive behavior initiated and received by males and females (cf. Harlow and Lauersdorf 1974, Mitchell and Tokunaga 1976, Baldwin 1968, 1969, 1971). Thus it was useful to compare the number of affinitive interactions initiated by males and females to the number received by each sex; for adult, juvenile, and infant classes. The following null hypothesis was tested:

> There is no significant difference between the amount of affinitive behavior initiated and that received by males and females.

By using two by two contingency tables derived from the frequencies in the final column and row of Table III, Fisher's Exact Probability test provided probabilities for these frequencies (Siegel 1956). On Table III(b) it can be seen that the hypothesis of no difference was rejected only for adults ($p < .008$). Adult males appeared to receive proportionately more affinitive behaviors than did adult females, relative to the number that each sex initiated. In contrast there was not a significant difference in the proportions of affinitive behaviors initiated and received by males and females for either juveniles or infants (Table III(b)).

Table III(b). Probabilities of Frequencies of Affinitive Interactions Initiated and Received by Males and Females of Each Age Class

	AM	AF	JM	JF	IM	IF
Initiates	527	486	238	387	264	302
Receives	709	531	171	251	117	136
	p=.008 n=2253*		p=.23 n=1047*		p=.5 n=819	

* Hypothesis of no preference for sex of partner rejected $p < .05$

To display these results graphically, the total number of affinitive interactions received and initiated by each age-sex class was calculated. These totals were then divided into relative percentages: affinitive interactions initiated, and those received by each age-sex class. Figure 1 is a bar graph showing how much affinitive behavior was initiated relative to that received by each of the seven age-sex classes. It can be seen that only adult (both male and female) monkeys received relatively more affinitive behaviors than they initiated.

Based on significant preferences for partners of one sex in affinitive interactions between age classes, the network of affinitive relationships is diagrammed in Figure 2. In this sociogram it can be seen that partners of the same sex were generally chosen for affinitive interactions.

Figure 1. Bar Graph showing Percentages of Total Affinitive Interactions Initiated and Received Within Each Age-Sex Class by Each Age-Sex Class (Bridging and Carrying Not Included)

(* Significant differences ($p < .05$) in proportion of behaviors initiated and received)

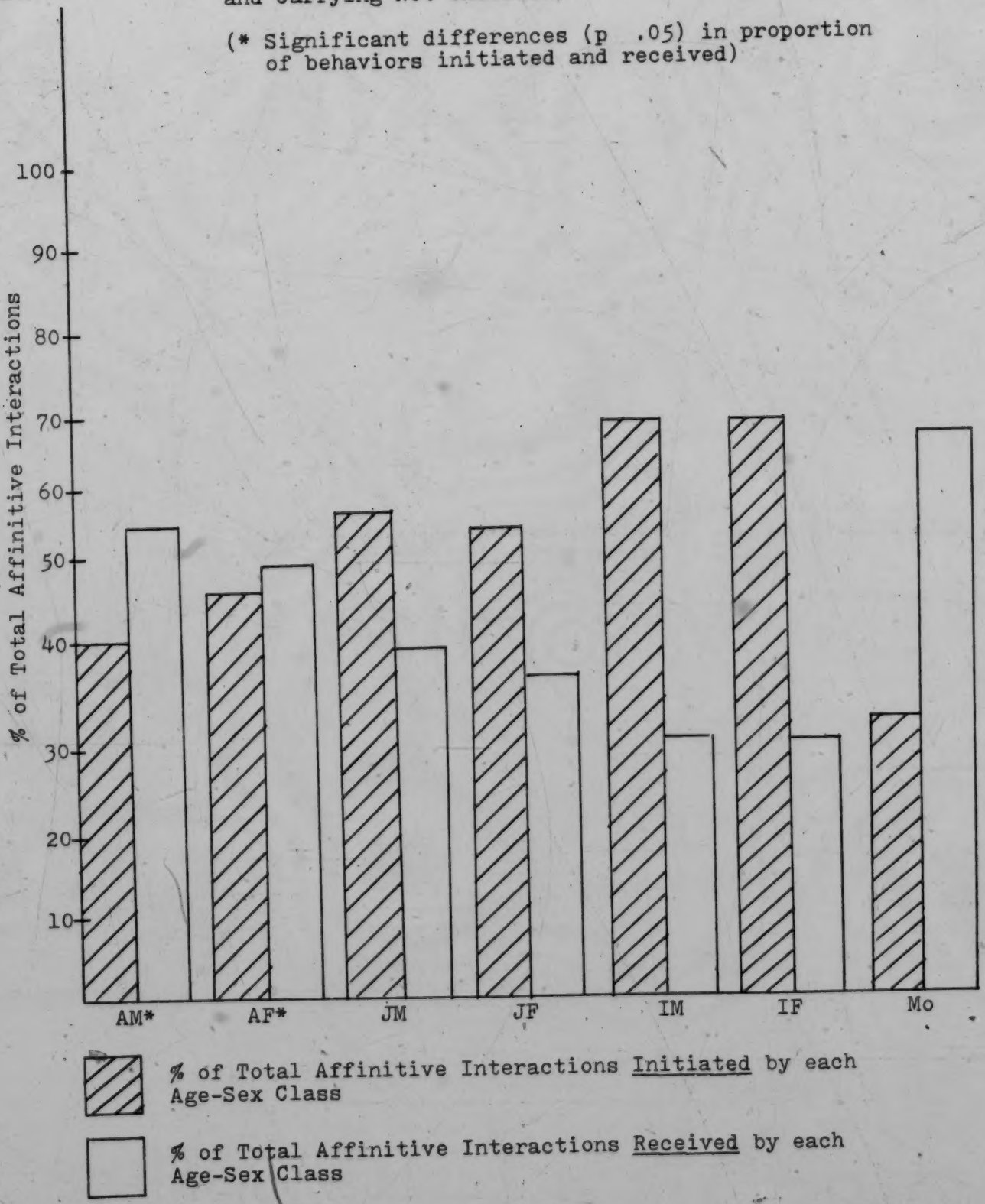
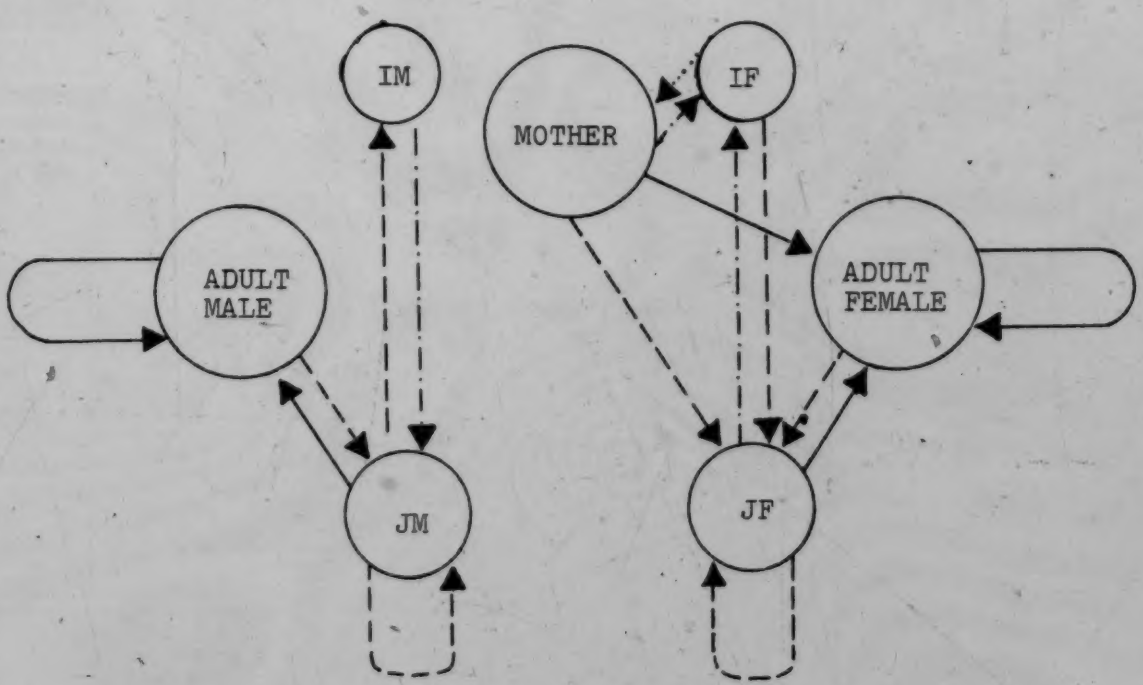


Figure 2. Sociogram showing significantly 'preferred' partners for affinitive interactions between and within adult, juvenile, and infant classes (Based on frequency of affinitive interactions)



'Preferred' sex of adult partner (based on frequency of affinitive interactions)

'Preferred' sex of juvenile partner

'Preferred' sex of infant partner

'Dotted' line indicates which infant class directed more affinitive interactions towards mother.

(Hypothesis that these preferences (except for mothers) were not significant, were rejected: $p < .05$) See Table IIIa

Sitting Together

Sade stated that "The observer identifies social relations within the group by the consistent close spacing of particular monkeys..." (Sade 1965: 3). The best measure of close spacing in spider monkeys who forage and move in loose flexible associations, is made at times when monkeys are sitting together. 'Sitting together' is a mutual state between monkeys and not an event. Therefore it was analyzed for duration, and frequency but not for direction as were the affinitive behaviors shown on Table III (cf. Altmann 1974).

Table IV gives frequencies and durations (in minutes) of 'sitting together' between and within age-sex classes. In addition the row percentages are shown, indicating the relative amounts of time spent by each age-sex class with each other. Sitting together includes the behavioral categories of 'sit in contact' and 'sit beside'.

By looking at the time spent by various age-sex classes with each other, it can be seen that possible preferences exist in the choice of partners for this contact. The following null hypothesis was tested:

> The time one individual spends sitting with another monkey of a given age class is not dependent on the sex of the other individual.

This hypothesis was tested using Fisher's Exact Probability (Siegel 1956) on the durations of 'sit together' between and within classes. Table IV(a) shows the contingency tables with the durations of this behavior, and the

Table IV. Frequencies and Durations in Minutes of Sitting Together Between and Within Age-Sex Classes

(Percentages refer to duration)

		AM	AF	JM	JF	IM	IF	Mo	Total Time Sit Together	Total Time Sit Alone
AM	Frequency	163	77	87	26	30	35	46	464	
	Duration	78	37	36	6	13	16	33	219	330
	% of Row	36	17	16	3	6	7	15		
AF	Frequency	77	66	17	54	6	14	4	238	
	Duration	37	20	16	23	-	10	18	124	354
	% of Row	30	16	13	19	-	8	14		
JM	Frequency	87	17	21	7	10	7	20	169	
	Duration	36	16	6	3	9	1	17	88	80
	% of Row	41	18	7	3	10	1	19		
JF	Frequency	26	54	7	15	3	11	18		
	Duration	6	23	3	7	2	10	5	56	82
	% of Row	11	41	5	12	4	18	9		
IM	Frequency	30	6	10	3	-	1	79	129	
	Duration	13	-	9	2	-	-*	30	54	27
	% of Row	24	-	17	4	-	-	55		
IF	Frequency	35	14	7	11	1*	4	259	331	
	Duration	16	10	1	10	-	1	94	132	34
	% of Row	12	8	1	8	-	1	71		
Mo	Frequency	46	4	20	18	79	259	11	437	
	Duration	33	18	17	5	30	94	6	203	85
	% of Row	16	9	8	2	15	46	3		

* Duration less than 30 seconds

Table IV(a). Probabilities of Durations of 'Sitting Together' Between and Within Age-Sex Classes

	AM	AF	JM	JF	IM	IF
AM	78	37	36	6	13	16
AF	37	20	16	23	0	10
	p=.41	n=172	p=.05	n=81*	p=.008	n=39*
JM			6	3	9	1
JF			3	7	2	10
			p=.12	n=19	p<.001	n=22*
IM					0	0
IF					0	1
					Not Testable	

* Hypothesis of no difference in time spent sitting with male and female partners, rejected ($p < .05$)

probability of these durations.

The hypothesis of no difference in time spent sitting with male and female partners was not rejected for adults, juveniles, or infants (Table IV(a)). This result indicated that adult males and females showed no significant preference for sitting with individuals of their own sex. However, both adult males and females spent a greater percentage of their time sitting with adult males, than with adult females (Table IV: 36% for adult males with males, 30% for adult females with males, and 17% for adult males with females, 16% for adult females with females).

The hypothesis of no preference for sex was rejected for sitting together between adults and juveniles, adults and infants, and juveniles and infants. In all these cases, where preferences were found, individuals of the same sex spent more time sitting with each other than they spent with members of the opposite sex. Preferences were especially marked in those instances where adults sat with juveniles. Juvenile males spent 41% (36 minutes) of their 'sitting together' with adult males, and only 16% (16 minutes) with adult females (Table IV). Conversely, juvenile females sitting with adult females accounted for 41% (23 minutes) of all the time juvenile females sat with other monkeys, in contrast to only 11% (6 minutes) spent with adult males.

In some ways, these results parallel those found in analysis of affinitive interactions where sexual segregation was found to structure affinitive relationships

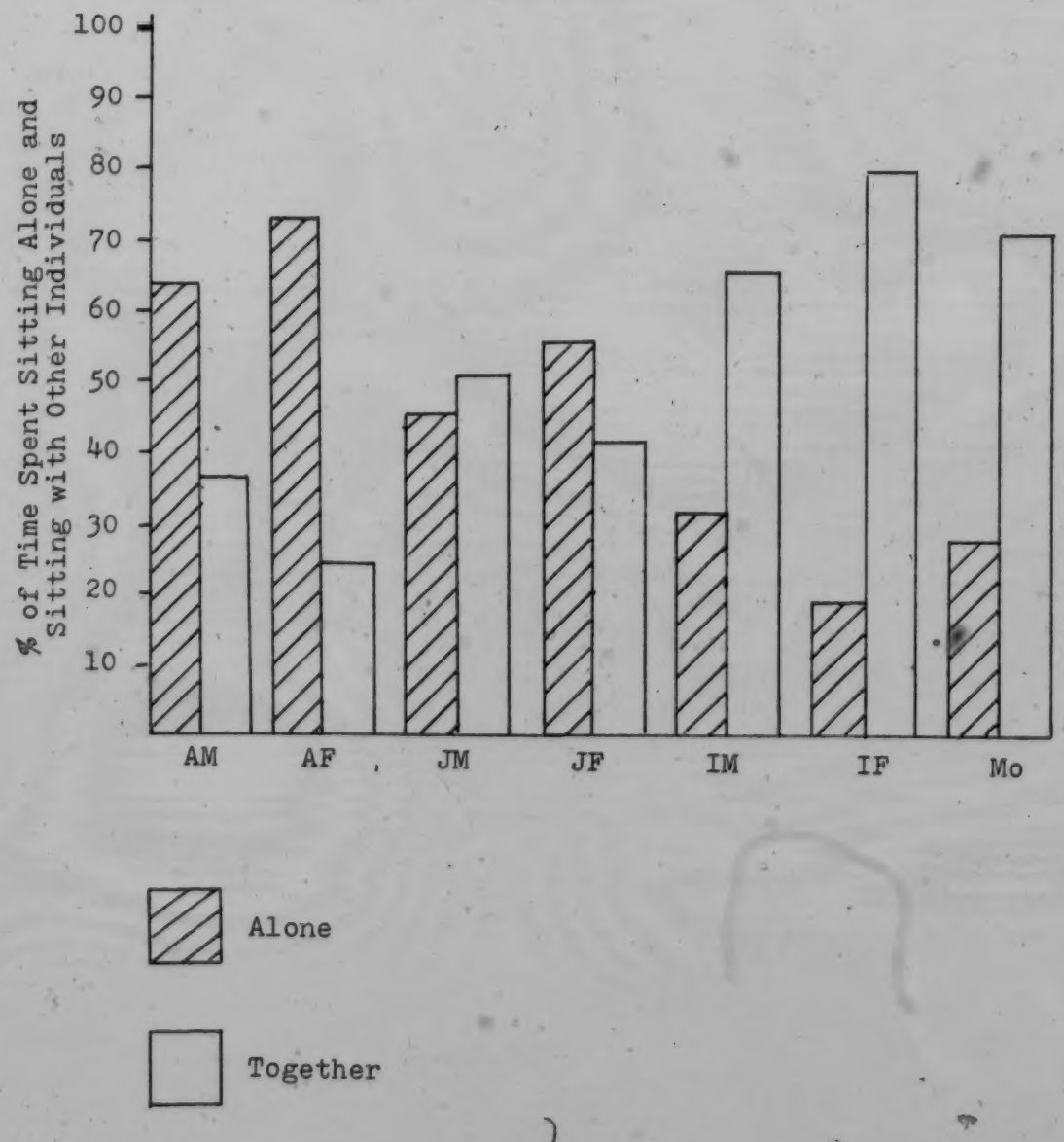
between and within age-sex classes. Sitting together, as an indication of close proximity and tolerance between individuals (Koyama 1973), revealed strong preferences between adults and juveniles for same sex individuals.

Unlike affinitive interaction patterns, however, adults did not show the strong sexual segregation during times of sitting together. Adult males still showed affinity for other adult males, but both adult females and mothers spent relatively more of their time sitting with adult males than they did with other adult females or mothers (Table IV, % of Row for AF and Mo).

Other patterns emerged when the total time each age-sex class spent sitting with others was compared to the time spent sitting alone by each class. Both the total times spent sitting alone and the times spent sitting together are shown on Table IV, (columns 8 and 9). Figure 3 is a bar graph which shows how much of the total time spent sitting by each age-sex class was alone, and how much (percentage of total) was with others. As might be expected, infants spent more time with others (usually their mothers) than they did alone. In accordance with results discussed later (section on mother-infant interactions) infant males spent a smaller percentage of their total 'sitting' time with another monkey (67%) than did infant females (80%).

Also of note is the fact that juvenile males who were generally engaged in fewer affinitive interactions than were juvenile females, spent relatively more of their

Figure 3. Percentages of Sitting Time Each Age-Sex Class Spent Alone and With Other Individuals



sitting time in close proximity with others. It has already been noted that 41% of the time juvenile males spent sitting with others was with adult males.

Juvenile females, on the other hand, spent less time sitting with others than they did sitting alone (Figure 3). The same is true for adult males and females, and adult females spent relatively more time sitting alone than did any other age-sex class. This result parallels the finding noted earlier, that adult females engaged in relatively more non-interactive behavior than did other age-sex classes.

Grooming

Grooming in macaques is said to be the best indicator of relationships between individuals of different ages and sexes (Sade 1965, Missakian 1973). It is also common in many primate species for adult females to initiate and receive more grooming than do adult males. This fact has been interpreted as an indication that female primates are more 'social' in their relationships than are males (Mitchell and Tokunaga 1976).

Analysis of affinitive interactions in this study has shown that this pattern did not characterize the affinitive interactions of spider monkeys at Tikal. The difference between male and female affinitive relationships was found in their direction, and not the degree to which males and females engaged in affinitive interactions.

Thus grooming interactions were analyzed separately to ascertain whether grooming relations show female spider monkeys to be more 'social' than are males.

Table V shows frequencies with which grooming occurred within and between age-sex classes. Row percentages are given as indices of how much each age-sex class distributed its grooming among the classes. Column percentages show what proportions of the total grooming received by each age-sex class was initiated by each other age-sex class.

As for affinitive interactions, the first question in the analysis of grooming was whether choices for partners were made on the basis of sex of the individuals. Using Fisher's Exact Probability (Siegel 1956), the following null hypothesis was tested:

> Grooming interactions between and within age classes are not dependent on the sex of the individuals involved.

Between adult males and females, grooming interactions indicated that there was no significant preference for partners of one sex, and the null hypothesis was not rejected (Table V(a)). It was seen in analysis of sitting together that adult males sat more with other adult males and adult females than did adult females with each other. On Table V it can be seen that grooming relations show the same trend. Adult males received more grooming from both adult females and other adult males, than did adult females.

Table V. Frequency of Grooming Between and Within Age-Sex Classes

INITIATES		RECEIVES AM	AF	JM	JF	IM	IF	Mo	Total Initiated
AM 32% sample	Frequency	19	13	11	7	5	1	5	61
	% of Row	31	21	18	11	8	2	8	
	% of Column	32	26	61	25	55	14	15	
	% of Total	9	6	5	3	2	1	2	30
AF 28% sample	Frequency	25	8	1	10	1	-	14	59
	% of Row	42	13	2	17	2	-	7	
	% of Column	13	16	6	38	11	-	42	
	% of Total	12	4	1	5	1	-	7	29
JM 9% sample	Frequency	5	2	4	-	-	-	2	13
	% of Row	38	15	31	-	-	-	15	
	% of Column	8	4	22	-	-	-	1	
	% of Total	2	1	2	-	-	-	1	6
JF 12% sample	Frequency	3	18	-	4	-	-	8	33
	% of Row	9	54	-	12	-	-	24	
	% of Column	5	37	-	14	-	-	24	
	% of Total	1	9	-	2	-	-	4	16
IM 6% sample	Frequency	-	-	-	-	-	-	1	1
	% of Row	-	-	-	-	-	-	100	
	% of Column	-	-	-	-	-	-	3	
	% of Total	-	-	-	-	-	-	1	-
IF 8% sample	Frequency	-	1	-	-	-	-	1	2
	% of Row	-	50	-	-	-	-	50	
	% of Column	-	2	-	-	-	-	3	
	% of Total	-	1	-	-	-	-	1	1
Mo 5% sample	Frequency	8	7	2	7	3	6	2	35
	% of Row	23	20	6	20	9	17	6	
	% of Column	13	14	11	25	33	86	6	
	% of Total	4	3	1	3	1	3	1	17
Total Received		60	49	18	28	9	7	33	204
% Total		29	24	9	14	5	3	16	

Table V(a). Probabilities for Occurrences of Grooming Between and Within Age-Sex Classes (All probabilities derived using Fisher's Exact Probability, Siegel 1956)

	AM	AF	JM	JF	IM	IF
AM	19	13	11	7	5	1
AF	25	8	1	10	1	0
	p=.12	n=65	p=.007	n=29*	p=.86	n=7
JM	5	2	4	0		
JF	3	18	0	4		
	p=.009	n=28*	No results	n=8		

* Hypothesis of no preference for grooming partners of one sex rejected ($p < .05$)

Table V(b). Probabilities for Frequency with which Grooming is Initiated and Received by Males and Females of Each Age-Sex Class (All probabilities derived using Fisher's Exact Probability, Siegel 1956)

	AM	AF	JM	JF
Initiates	61	59	13	33
Receives	60	49	18	28
	p=.31	n=229	p=.19	n=92

The hypothesis of no preference for grooming individuals on the basis of their sex was rejected for grooming interactions between adults and juveniles (Table 5 (a)). As was found for other affinitive interactions and sitting together, in grooming each other, adults and juveniles showed tendencies to choose same-sex partners. Grooming relations of juvenile females with adult females were found to be especially strong. They accounted for 54% of all grooming performed by juvenile females, while only 9% of this total was with adult males. Juvenile males groomed adult males in 38% of all their grooming interactions, while adult females received only 15% of all juvenile male grooming (Table V).

Given that grooming between adult males and females did not reveal significant differences in choice for partners of the same sex, it was of interest to ascertain whether the amounts of grooming initiated and received by adult males and females differed. A null hypothesis was formulated as follows:

> Males and females do not receive and initiate different proportions of grooming interactions.

Using Fisher's Exact Probability (Siegel 1956), and the contingency tables in Table V(b), this hypothesis was tested. No significant difference was found between the proportions of grooming initiated and received by adult males and females, or for juveniles (Table V(b)). The hypothesis was not rejected in either case.

In some species of baboons it is the duration and

not frequencies of grooming bouts that differ between males and females (Mitchell and Tokunaga 1976). Analyses of variance of the mean lengths of grooming bouts between and within age-sex classes of spider monkeys showed significant differences in these lengths for adult female grooming interactions. The mean durations for grooming bouts initiated by adult females are shown on Table VI. Adult females groomed adult males in bouts almost equal in length to those for other adult females (Table VI). However, adult females groomed juvenile females and mothers with infants for significantly longer periods than those in which they groomed juvenile or infant males ($df=5$, $p=.0018$).

The picture of preferences in grooming relations within and between age-sex classes is illustrated graphically in Figure 4. This sociogram shows the direction of grooming, where significant preferences for partners of one sex were found. Grooming preferences of mothers (with infants) were not tested. Thus the grooming relations depicted in Figure 4 represent the more frequent choice made by mothers in grooming each age class. The sexual segregation which was so clearly revealed by a diagram of affinitive interactions (Figure 2) does not characterize the grooming relationships shown in Figure 4. Only in grooming between adults and juveniles is there clear preference for members of the same sex.

Table VI. ANOVA of Mean Deviations for Grooming Bouts in Which AF Groom other Age-Sex Classes

Age-Sex Class Receiving Grooming from AF	Frequency	Mean Length of Bout (Secs.)
AM	20	32
AF	6	33
JM	1	4
JF	1	117
IM	1	30
IF	0	0
Mo	9	71

df 5

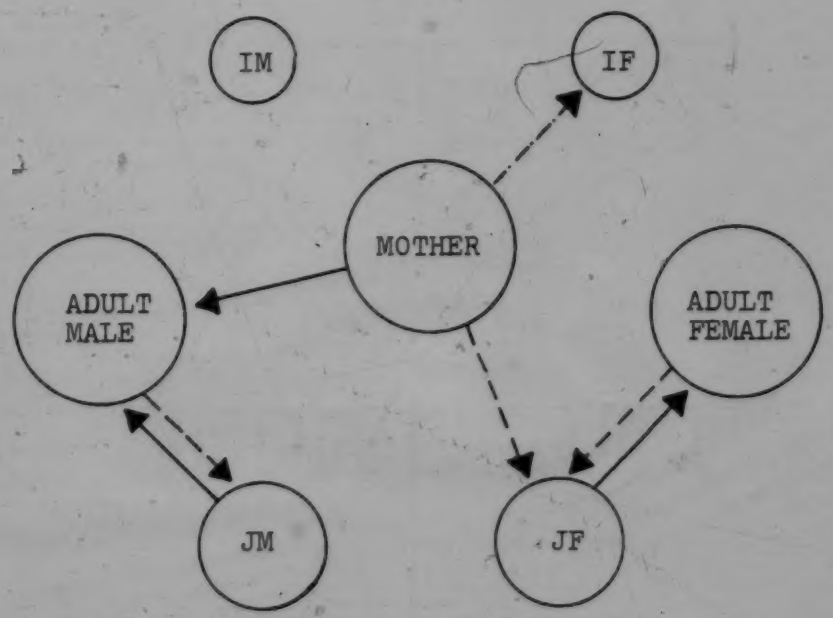
F 4.949

p 0.0018

Subsets 1 IM JM AM AF

2 AM AF Mo JF

Figure 4. Sociogram showing significantly 'preferred' partners for grooming interactions for adult, juvenile and infant classes (based on frequency of initiated grooming interactions)



Fewer than 3 grooming interactions not recorded.

——→ 'Preferred' sex of adult partner (based on frequency of grooming interactions)

– – – –→ 'Preferred' sex of juvenile partner for grooming

–·–·–·→ 'Preferred' sex of infant partner for grooming

·····→ Hypotheses that these 'preferences' not statistically significant rejected ($p < .05$)

(Mother's preferences indicate most frequent grooming interactions with each age class)

Agonistic Interactions

Table VII gives the frequencies with which agonistic interactions occurred within and between the seven age-sex classes. Agonistic refers to 'chase', 'attack', 'being retreated from', and 'displace', according to the definition given in the methods section.

Table VII also provides row percentages which indicate how much of the agonistic behavior initiated by each age-sex class was received by the seven age-sex classes. Similarly column percentages show how much of all agonistic behavior received by one class was initiated by each of the seven age-sex classes.

There are indications in Table VII that agonistic interactions were more frequent between individuals of certain ages and sexes. These led to the formulation of the following null hypothesis:

> Agonistic interactions occur between and within age classes independent of the sexes of individuals participating.

Fisher's Exact Probability (Siegel 1956) was used to test this hypothesis for agonistic interactions between adults, between adults and juveniles, and between juveniles (Table VII(a)). Frequencies of agonistic interactions between other classes were not tested because of insufficient data (Table VII).

Agonistic interactions between adults, and those between juveniles, provided no evidence that would reject the null hypothesis. However, the hypothesis of independence

Table VII. Frequency of Agonistic Encounters Between and Within Age-Sex Classes (Chase, Attack, Being Retreated from, Displace)

INITIATES		RECEIVES AM	AF	JM	JF	IM	IF	Mo	Total Initiates
AM 32% sample	Frequency	19	79	18	9	2	2	6	135
	% of Row	14	58	13	7	2	2	4	
	% of Column	68	71	68	50	22	22	40	
	% of Total	9	36	8	4	1	1	3	62
AF 28% sample	Frequency	1	16	0	4	2	2	4	29
	% of Row	3	55	-	14	7	7	14	
	% of Column	4	14	-	22	22	22	27	
	% of Total	-	7	-	2	1	1	2	13
JM 9% sample	Frequency	0	5	2	1	1	1	0	10
	% of Row	-	50	20	10	10	10	-	
	% of Column	-	4	7	5	11	11	-	
	% of Total	-	2	1	-	-	-	-	5
JF 12% sample	Frequency	0	4	1	3	1	2	1	12
	% of Row	-	33	8	25	8	17	8	
	% of Column	-	4	4	17	11	22	7	
	% of Total	-	2	-	1	-	1	0	6
IM 6% sample	Frequency	0	2	2	0	0	0	0	4
	% of Row	-	50	50	-	-	-	-	
	% of Column	-	2	7	-	-	-	-	
	% of Total	-	1	1	-	-	-	-	2
IF 8% sample	Frequency	0	0	0	0	0	0	0	0
	% of Row	-	-	-	-	-	-	-	-
	% of Column	-	-	-	-	-	-	-	-
	% of Total	-	-	-	-	-	-	-	-
Mo 5% sample	Frequency	8	5	4	1	3	2	4	27
	% of Row	30	18	15	4	11	7	15	
	% of Column	29	4	15	5	33	22	27	
	% of Total	4	2	2	-	1	1	2	12
Total Received		28	111	27	18	9	9	15	217
% Total		13	52	12	8	4	4	7	Total

Table VII(a). Probabilities of Frequencies of Agonistic Interactions Between and Within Age-Sex Classes (All probabilities derived using Fisher's Exact Probability, Siegel 1956)

	AM	AF	JM	JF
AM	19	79	18	9
AF	1	16	0	4
	p=.15	n=115	p=.02	n=31*
JM	0	5	2	1
JF	0	4	1	3
	No results		p=.37	n=7

Table VII(b). Probabilities of Frequencies of Agonistic Interactions Initiated and Received by Each Age Class

	AM	AF	JM	JF
Initiated	135	29	10	12
Received	28	111	27	18
	p < .001	n=303*	p=.19	n=67

* Hypothesis of no difference in proportion of agonistic interactions initiated and received by males and females of each age class.

of sex was rejected for agonistic interactions between adult and juvenile monkeys (Table VII(a)). Adult males directed 13% of their agonistic behaviors at juvenile males, and only 7% at juvenile females. Adult females directed no agonism at juvenile males, but 14% of their total was toward juvenile females. Thus the relationships between adults and juveniles of the same sex were found to be multi-dimensional, consisting of both affinitive and agonistic components.

The total number of agonistic interactions initiated by adult males and adult females was compared to those received by each of these classes, to test the null hypothesis:

> There is no significant difference in the relative amount of agonism initiated and received by males and females.

The results obtained by testing the numbers of agonistic interactions initiated and received by males and females are shown on Table VII(b). Juvenile males and females did not show a difference in the amount of agonistic behavior they initiated relative to that they received, and therefore the hypothesis was not rejected.

However, adult males and females showed significant differences in the number of agonistic interactions they initiated and received (Table VII(b)), and the null hypothesis was rejected. Upon examination, the difference lies in the fact that adult males initiate far more agonistic interactions than they receive; while the reverse is true

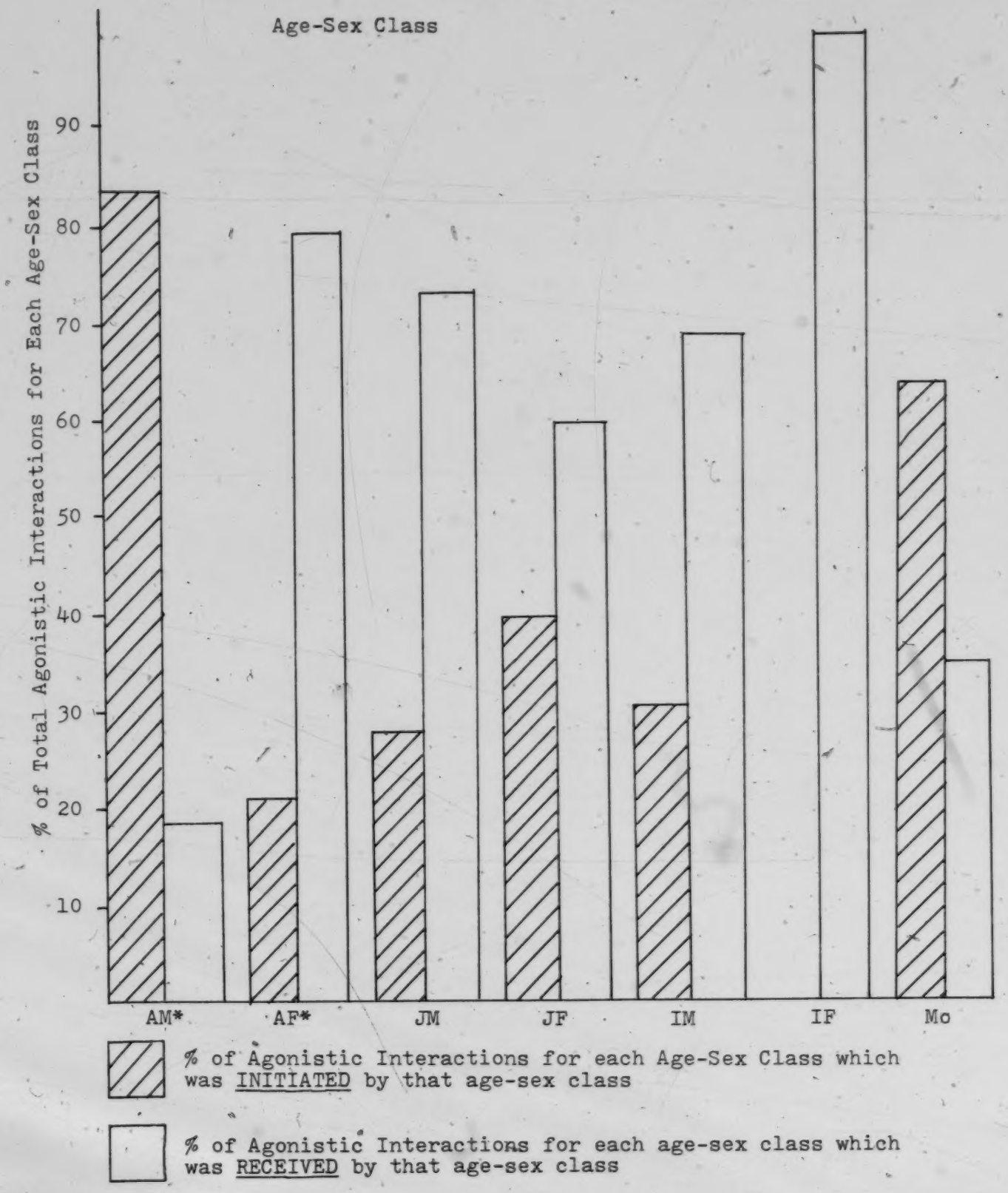
for adult females, who initiate few, but receive many agonistic behaviors.

Of note is the high frequency of agonistic behaviors directed by adult males at adult females. Thirty of these male-female interactions took the form of vigorous and intimidating chases by the males. Qualitative field notes showed that these incidents often involved a small group of independently locomoting males who performed these chases as displays. While it appeared that the females were perhaps in the way of the male party moving along an arboreal pathway or in desired food or sitting trees, the females were rarely displaced entirely by the males. Generally one female received the brunt of the chasing, while the others scattered, slightly out of the direct paths of the males.

Figure 5 is a bar graph showing the amount of agonistic behavior initiated relative to that received by males and females of each age-sex class. One may observe the fact that adult males initiated significantly more agonistic interactions than they received, relative to adult females who received more agonism than they initiated.

Many of the adult agonistic interactions were with other adults. It was useful to show how much agonism was initiated and received by adult males and females, relative to affinitive interactions between them. This comparison is shown graphically in Figure 6. Only in the case of adult male-adult female interactions was there more agonistic behavior received than affinitive. In all other

Figure 5. Bar Graph showing Proportions of Agonistic Interactions Initiated and Received by Each Age-Sex Class



instances, more affinitive interactions were initiated than were agonistic interactions.

Other Behaviors

The agonistic interactions discussed up to this point correlate with what Cant (1976) termed 'short distance agonistic behavior' and what Klein (1974) defined as 'altercations' and 'supplantations'. These are encounters between individuals usually within 15 m of each other. Both Cant (1976) and Klein (1974) pointed to the frequent occurrence of male aggression against adult females in these encounters, as found here. They also suggested that these occurred within social groups.

Such short distance agonistic behavior can be distinguished from 'long distance agonism' (Cant 1976) and 'confrontations' (Klein 1974). The latter involved whole parties of monkeys, performing displays toward other groups. Such displays may be territorial in nature, and appear to space or mark ranges of localized populations of spider monkeys (Klein 1974; Eisenberg 1976). Display howl used here, corresponds to such 'long distance agonism'. Frequencies with which individuals were recorded performing display howl behaviors are recorded in Table VIII. Display howl was performed only by adult males.

In the 18 weeks of study, this display of agonism was seen being performed on several occasions, by parties of varying sizes and with different degrees of energy output.

Figure 6. Bar graph showing percentages of directed agonistic and affinitive interactions between adult males and adult females

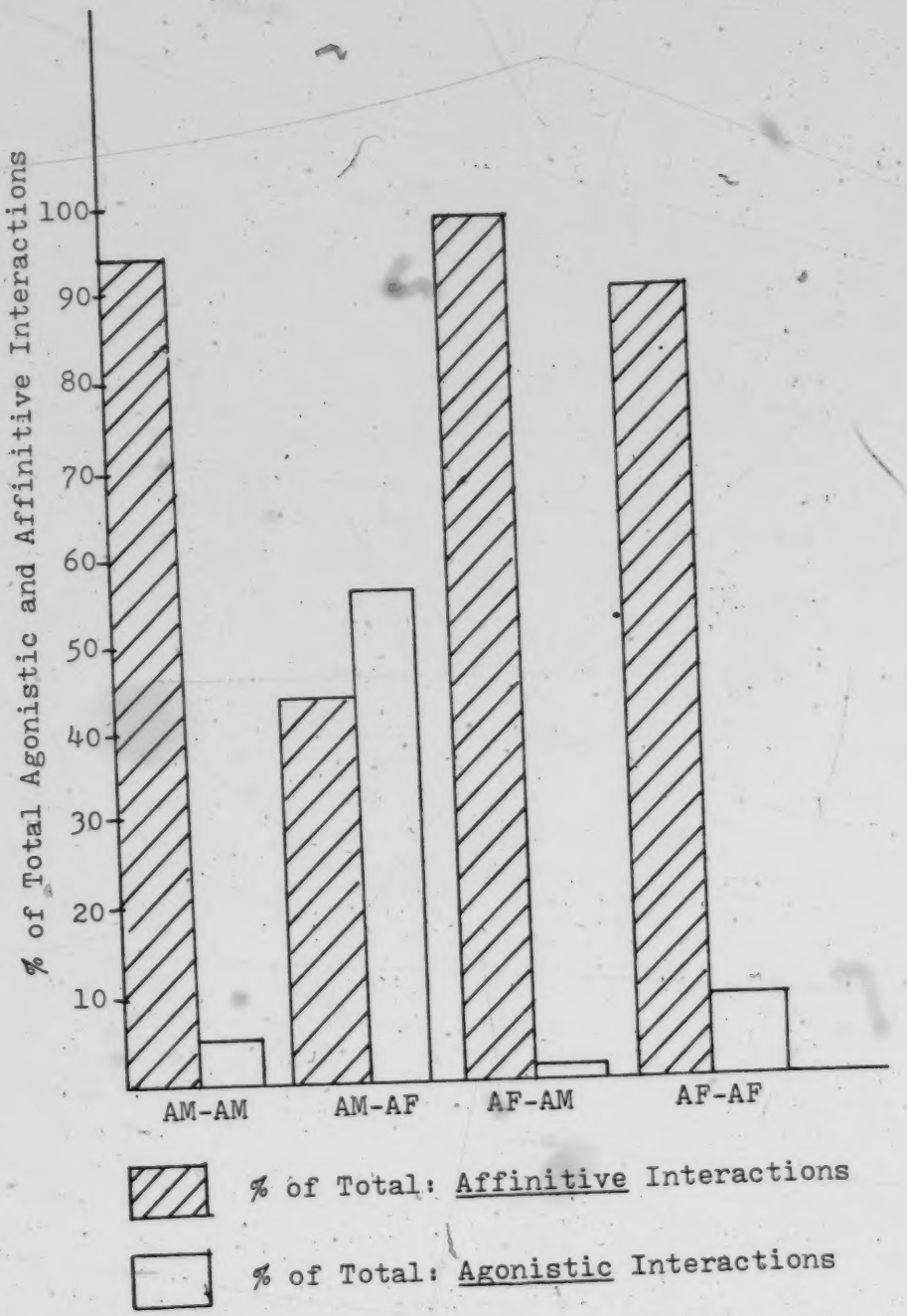


Table VIII. Frequency of Other Actions

		No. of Focal Animals Sampled	Vocalize*	Yelp	Branch-Shake	Display-Howl	Look Around
AM	Frequency	570	258	8	37	20	304
	% Total	32	22	22	22	100	50
AF	Frequency	507	540	18	76	0	164
	% Total	28	46	50	44	-	27
JM	Frequency	168	88	1	14	0	57
	% Total	9	8	3	8	-	10
JF	Frequency	220	122	4	31	0	33
	% Total	12	10	11	18	-	5
IM	Frequency	134	30	0	4	0	4
	% Total	8	3	-	2	-	1
IF	Frequency	105	24	0	4	0	5
	% Total	6	2	-	2	-	1
Mo	Frequency	89	106	5	5	0	35
	% Total	5	9	14	3	-	6
	Total	1793	1168	36	171	20	602

* Vocalize here includes general whinny Vocalizations, Grunt, Distress bark, Agonistic bark, Growl, Whine.

However, as noted in Table VIII, the display itself was exclusively done by adult males. Associations of adult females and mixed age-sex classes were often in the vicinity where these displays were occurring.

As described in the ethogram, this display involved a series of consistent motor patterns: leaping vigorously from branch to branch, branch-shaking, mounting other males, and shrill howls. The males frequently performed these actions in a particularly tall bare tree affording them a good view of the surrounding canopy as they looked intently off into the distance.

While the display howl as a form of long distance agonism was limited in its occurrence to adult males, other agonistic behaviors involving threats were not. Branch-shaking was a behavior most often noted as a response of the monkeys to human observers, and it seemed to be performed as a threat to drive away the intruders. Frequencies of branch-shaking are shown on Table VIII. Adult females accounted for 44% of all branch-shaking threats, adult males 22%, and juvenile females 18%. When compared to the percentages of individuals sampled in each age-sex class, it can be seen that adult and juvenile females accounted for relatively more of this behavior than might have been expected.

Yelping is a form of vocal display which indicated a high level of arousal in the monkeys, with no obvious show of directed agonism. Yelping involves rapid repetitive

barklike vocalizations usually emitted simultaneously by several monkeys sitting together in a mixed party. Klein (1974) described a similar phenomenon in females, 'ook-barking', which occurred often in the presence of adult males. Adult females were responsible for 50% of all yelping observed, adult males only 22% (Table VIII).

In addition, females were found to be more vocal in general, than were adult males. Figures in Table VIII (column 1) show that adult females accounted for 46% of all vocalizations recorded; adult males accounted for only 22%. These percentages are proportionately higher than expected, given the ratios of adult females sampled in these age-sex classes, shown in Table VIII. As mentioned previously, vocalizations include 'vocalize', 'grunt', 'distress bark', 'agonistic bark', 'growl', and 'whine'. Yelp involved an attitude with rigid postures and was more ritualized than these 'vocalizations'.

Contact calls were tabled separately (Table IX), since direction is an important dimension in the analysis of these calls. While adult females emitted more 'vocalizations' than did adult males, contact calls which involve a call and an answering response, do not show this differentiation based on sex. Adult males gave 85 calls, 45% of these with other adult males; while adult females gave 82 contact calls, and 29% of these were with other adult females.

It may be that distinction in the behavioral profiles of males and females corresponds to a separation

Table IX. Frequency of Contact Calls Between and Within Age-Sex Classes

		AM	AF	JM	JF	IM	IF	Mo	Unknown	Total
AM	Frequency	38	10	3	0	0	0	5	29	85
	% of Row	45	12	3	-	-	-	6	34	
	% of Column	43	10	16	-	-	-	16	33	
	% of Total	10	3	1	-	-	-	1	8	23
AF	Frequency	5	24	6	14	0	0	2	31	82
	% of Row	6	29	7	17	-	-	2	38	
	% of Column	6	24	32	48	-	-	6	36	
	% of Total	1	7	2	4	-	-	1	9	23
JM	Frequency	1	7	0	1	0	0	1	8	18
	% of Row	6	39	-	6	-	-	6	44	
	% of Column	1	7	-	3	-	-	3	9	
	% of Total	-	2	-	-	-	-	-	2	5
JF	Frequency	0	6	0	0	0	0	4	5	15
	% of Row	-	40	-	-	-	-	27	33	
	% of Column	-	6	-	-	-	-	13	6	
	% of Total	-	2	-	-	-	-	1	1	4
IM	Frequency	0	0	0	0	0	0	0	0	0
	% of Row	-	-	-	-	-	-	-	-	
	% of Column	-	-	-	-	-	-	-	-	
	% of Total	-	-	-	-	-	-	-	-	-
IF	Frequency	0	0	0	0	0	0	0	0	0
	% of Row	-	-	-	-	-	-	-	-	
	% of Column	-	-	-	-	-	-	-	-	
	% of Total	-	-	-	-	-	-	-	-	-
Mo	Frequency	1	3	1	7	2	6	1	14	35
	% of Row	3	8	3	20	6	17	3	40	
	% of Column	1	3	5	24	67	100	3	16	
	% of Total	-	1	-	2	1	2	-	4	10
Unknown	Frequency	43	49	9	7	1	0	19	0	128
	% of Row	34	38	7	5	1	-	15	-	
	% of Column	49	49	47	24	33	-	59	-	
	% of Total	12	13	2	2	-	-	5	-	35
	Total	88	99	19	29	3	6	32	87	363
		24	27	5	8	1	2	9	23	

in the nature and function of the social tasks represented by 'yelp', 'display howl', 'branch shake', and 'vocalize'. Gartlan (1968) attached discrete categories to similar behaviors in vervet monkeys, basing his categories on functions of the behaviors. In addition to the territorial display of adult males, he pointed out that adult males also maintain social vigilance activities in the form of 'looking out'. Male spider monkeys at Tikal did more of this than did females. While adult males accounted for 32% of the individuals sampled, adult males accounted for 50% of all 'looking out' recorded (column 5, Table VIII).

Pectoral Sniff and Embrace

Another behavior for consideration is that which Klein and Klein (1971) described as the 'pectoral sniff and embrace'. This stereotyped action, which is apparently unique to spider monkeys, corresponds to a similar sequence of interactions, 'genital display and genital sniff', described by Eisenberg (1976). Klein (1972) suggested that this behavior occurred most often as a greeting gesture between two individuals who had been separated from each other, but who were familiar with each other. Eisenberg (1976) felt that the action was a form of dominance definition between adult and juvenile males.

Adult males performed most of these embraces, accounting for 76% of the cases recorded (Table X). Klein's (1972) view of this behavior is substantiated

Table X. Frequency of Pectoral Sniff and Embrace Between and Within Age-Sex Classes

	AM	AF	JM	JF	IM	IF	Mo	Total
AM	37	0	3	0	0	0	2	42
% of Total	76	0	6	0	0	0	4	86
AF	0	1	1	2	0	0	0	4
% of Total	0	2	2	4	0	0	0	8
JM	3	1	2	0	0	0	0	6
% of Total	6	2	4	0	0	0	0	12
JF	0	2	0	0	0	0	0	2
% of Total	0	4	0	0	0	0	0	4
IM	0	0	0	0	0	0	0	0
% of Total	0	0	0	0	0	0	0	0
IF	0	0	0	0	0	0	0	0
% of Total	0	0	0	0	0	0	0	0
Mo	2	0	0	0	0	0	1	3
% of Total	4	0	0	0	0	0	2	6

TOTAL = 49

somewhat by observations at Tikal. Qualitative descriptions of these incidents generally show that it occurred when a new monkey entered an area, or when one monkey was proceding directly towards or in front of another, en route to a feeding or resting spot. Because dominance was not clearly documented in this study, it is unclear whether pectoral sniff and embrace behavior was indeed a form of dominance definition as suggested by Eisenberg (1976).

Play

Play interactions among spider monkeys at Tikal provided the monkeys (and the observers) with many hours of diversion. The frequencies and duration of all play bouts ('play', 'grapple','play chase') are presented in Table XI. The final column of Table XI shows the relative amounts of observation time for each age-sex class. These may be compared to the figures in the adjacent column which gives percentages of all observed play for respective age-sex classes, to show that play involved juveniles and infants to a greater extent than it did adult males and females. For instance, adult males accounted for only 6% of all play interaction, but 32% of total sampling time. Infant males accounted for 22% of all play, and only 6% of the sampling time.

In this study duration is felt to be a more accurate index of the relative importance of play interactions between and within age-sex classes than frequency since actual play

Table XI. Frequency and Duration of Play Interactions (Play, Play Chase, Grapple) Between and Within Age-Sex Classes

								Total Frequency and Duration of Play	% Play	% Sample Time
AM	Frequency	19	14	33	15	12	5	0	98		
	Duration (Seconds)	999	341	1059	517	322	155	0	3393	6	32
	% of Row	30	10	31	15	9	5	0			
AF	Frequency	14	32	26	52	15	6	1	146		
	Duration (Seconds)	341	774	561	1433	487	213	3	3815	7	28
	% of Row	9	20	15	37	13	6	0			
JM	Frequency	33	26	20	96	51	37	12	275		
	Duration (Seconds)	1059	561	683	3742	2658	1888	465	11056	20	9
	% of Row	10	5	6	34	24	17	4			
JF	Frequency	15	52	96	83	70	54	3	373		
	Duration (Seconds)	517	1433	3742	3066	5420	2050	104	16332	29	12
	% of Row	3	9	23	19	33	12	1			
IM	Frequency	12	15	51	70	13	50	17	228		
	Duration (Seconds)	322	487	2658	5420	386	2496	647	12416	22	6
	% of Row	3	4	21	44	3	20	5			
IF	Frequency	5	6	37	54	50	19	6	177		
	Duration (Seconds)	155	213	1889	2050	2496	689	136	7627	14	8
	% of Row	2	3	25	27	33	9	2			

Table XI. Frequency and Duration of Play Interactions (Play, Play Chase, Grapple) Between and Within Age-Sex Classes (continued)

								Total Frequency and Duration of Play	% Play	% Sample Time
Mo	Frequency	0	1	12	3	17	6	0	39		
	Duration (Seconds)	0	3	465	104	647	136	0	1355	2	5
	% of Row	0	0	34	8	48	10	10	-	-	-

bouts, with the frequent intervals of resting, sparring, chasing and grappling, are difficult to count. Interruptions in play make frequent counts unreliable measures of how much play is actually occurring.

Table XI gives frequencies and duration for all play between and within age-sex classes. As well, the relative percentages of time spent by each age-sex class in play with each of the seven classes are given. Patterns in play interactions between and within these classes are analyzed by comparing these durations.

The greatest amount of play was observed between juvenile females and infant males, who were recorded in play activities with each other for 5420 seconds (90 minutes). This total represented 33% of all the time spent by juvenile females in play, and 44% of that spent by infant males in play interactions. Juvenile males played with juvenile females for less time (3742 seconds, 62 minutes), but this total accounted for 34% of all time spent by juvenile males in play.

Play between pairs of juvenile females appeared to be more common than was play between pairs of juvenile males. Juvenile females spent 3066 seconds (51 minutes) or 19% of their time in play with each other. In contrast, pairs of juvenile males spent only 683 seconds (11 minutes) or 6% of their time in play with each other.

Neither infant males nor infant females spent much time playing with same-sex infants. However, infant males

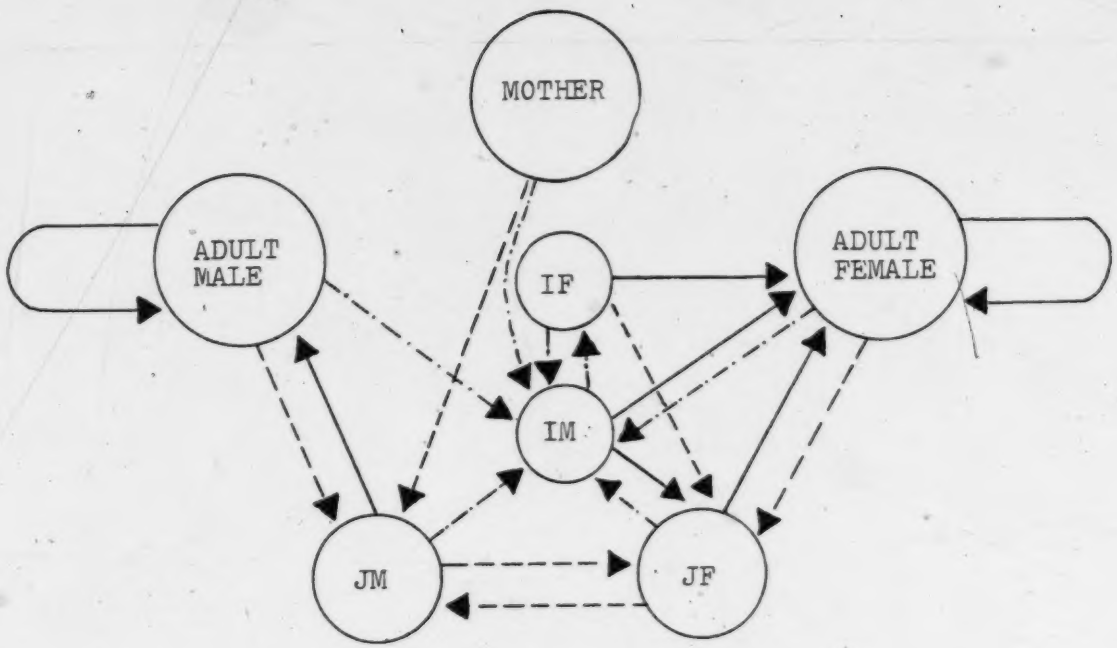
were focal in the play interactions of juvenile males, juvenile females, and infant females. Play with infant males accounted for the highest percentages of the play performed by each of these classes (34% of juvenile male play, 33% of juvenile female play, and 33% of infant female play was with infant males: Table XI).

Figure 7 is a sociogram which graphically illustrates the directions of play between and within age classes. The predominance of infant males in the network of play relations is shown in this diagram. 'Preferences' for play partners indicated in Figure 7 are drawn between age classes to the sex class for which the most time in play was recorded.

Mother-Infant Interactions

As mentioned in the Methods section, unequal numbers of infant males and infant females were sampled through focal animal sampling, due largely to the difficulties of positively sexing infant males. Thus 105 infant males and 26 mothers with infant males were sampled, a total of 131 mother-infant male dyads. This total is somewhat fewer than the 197 mother-infant female dyads sampled: 134 infant females and 63 mothers with infant females. Thus interactions between mothers with female infants should account for 60% of those between mothers and infants, while 40% of these should be between mothers and infant males, if there is no difference in the frequency with which mothers interact with male and female infants.

Figure 7. Sociogram showing 'preferred' sex class for play interactions between and within adults, juveniles and infants (Based on longest duration of play with each age-sex class. %)



'Preferred' sex class for play interactions with adults

'Preferred' sex class for play interactions with juveniles

'Preferred' sex class for play interactions with infants

Fewer than 5 seconds of play (Mother-adult) not noted

By looking at Table XII, it can be seen that for all forms of mother-infant interactions except grooming, those between infant females and mothers accounted for more than 60% of the total, and interactions between infant males and mothers accounted for less than the expected 40% of the total. Carry and Bridge For are both behaviors which require a certain degree of initiation by the mother. Infant females received proportionately more of these than did infant males, considering both durations and frequencies of these behaviors. The same pattern of mothers interacting less with infant males than females is seen for mothers eating in contact (with infants on their backs) and sitting with infants.

Mothers groomed male infants relatively more often than might have been expected, given the patterns noted above (56% of the total grooming bouts between mothers and infants was with infant males). However, it can be seen that grooming did not occur with great frequency between mothers and infants, since only 16 incidents were recorded (Table XII).

Note should also be made of patterns of affinitive interactions between infants and other age-sex classes, noted in Table III. Interactions between adult and infants showed that relationships between these age classes did not reflect stronger affinitive bonds between individuals of the same sex. Both infant males and females interacted more with adult males than with adult females (other than

Table XII. Mother-Infant Interactions

ACTION	Expected 40% Infant Male Frequency (% total) Duration (% total)	Expected 60% Infant Female Frequency (% total) Duration (% total)	Total
Mother Carries	97 times (31%) 64 mins. (33%)	218 times (69%) 130 mins. (67%)	315 times 194 mins.
Mother eats with infant on her back	9 times (15%) 5 mins. (15%)	51 times (85%) 29 mins. (85%)	60 times 34 mins.
Mother Bridges	3 times (30%)	7 times (70%)	10 times
Mother sits With	79 times (23%) 30 mins. (25%)	259 times (77%) 91 mins. (75%)	338 times 121 mins.
Mother Grooms	9 times (56%)	7 times (44%)	16 times
Mother is Groomed by	1 time (33%)	2 times (67%)	3 times

mothers). Affinitive interactions between infants and juvenile did show stronger affinitive relationships between same-sex partners.

Sexual Behavior

During the 4 months of field observations the researchers witnessed 3 full copulation sequences, which conformed in nature, duration and context to those described by Klein (1971). These 3 incidents were recorded at varying times of the day, and under different circumstances. The first was seen on March 28th at 621 h., and it was 14 minutes from the initial approach and insertion until the animals broke contact with each other and moved off in close association. They were followed by us for about 10 minutes, at which point the female joined another group of foraging females and the male moved off out of sight.

The second copulation occurred on April 18th at 1620 h. in a very different context, one of vigorous afternoon foraging and interaction. The male had just previously been observed displacing the female in a series of rather subtle interactions. The sequence of interactions was recorded in the field notes in the following way:

1639 h. 0 seconds: Adult male foraging in tree, 1 adult female and adult male also foraging in same tree.

46 seconds: Adult male locomotes, at which point he appears to have become aware of nearby adult female. Second adult

male has moved out of tree.

49 seconds: Adult female retreats from the adult male left in tree, and sits nearby.

54 seconds: Adult male and adult female are now sitting in tree, separated by about 2 meters.

113 seconds: Adult male is approached by adult female who sits beside him.

117 seconds: He touches her clitoris and sniffs his finger repeatedly.

281 seconds: Copulation begins as male moves his ventrum against female's dorsum, wraps his legs around her, pulls her in to his ventrum by holding her around the stomach tightly with both his forearms. Tail is also wrapped around her stomach. At the time of insertion the male is holding the female's clitoris with his left hand. She looks back at him, he manipulates her by pulling harder with his arms.

436 seconds: Adult male breaks contact with adult female and moves away one meter to sit alone. Both sit.

493 seconds: Adult female whinnies, adult male moves toward her at this time.

507 seconds: Adult male briefly chases adult female; she retreats.

517 seconds: Adult female sits and adult male moves along behind.

525 seconds: Adult male briefly chases adult female, who retreats whining.

589 seconds: Adult female sits and adult male approaches from behind, until he moves close enough to her (2 meters), that she once again begins whining and retreats.

This sequence was repeated until 746 seconds, (12.4 minutes) when they moved out of sight.

At this time the adult female was still showing apparent apprehension whenever the male was within 2 meters of her. There was a general movement of monkeys out of this area during this time.

The third copulation was observed about 1 week later, on April 29th at 0830 h., in a context of relaxed morning resting. Neither monkey appeared to be paying much attention to the other prior to the observed copulation; although the researchers were not watching the preceding events closely, for precisely this reason. From beginning to end the actual copulation lasted 668 seconds. During this time the adult male occasionally withdrew from the female between thrusts, a pattern not seen in the other two copulations. He embraced the female in a similar manner to that described previously, and the female looked back at

him with an open mouth. At the point of apparent ejaculation (547 seconds), the male pulled the female towards him very closely using both his arms and legs wrapped around her ventrum, and he did not release his hold until about 668 seconds. At this time she sat beside him (1-2 meters away); and rubbed her clitoris vigorously with her hand, then on the branch.

Another possible sequence of sexual behavior was observed in which a male and female groomed each other, presented their genitalia to each other, and sat together from 1043 h., when observations began, until 1122 h., when they were lost in a larger progression of monkeys moving off. In addition a similar sequence was seen between two juvenile males, on January 30th at 1600 h. They were first sighted in a presumed copulatory position, one holding the other from behind and performing possible thrusting motions. In between foraging bouts, place-sniffing, and following each other, this embrace was repeated 2 more times until 1646 h., at which time the researchers lost contact with them as they moved off in close association with each other.

Summary of Results

Action Patterns

Of all recorded actions, 12,679 (68.5%) were non-interactive behaviors and 5843 (31.5%) were interactions between two individuals. Adult females accounted for a higher percentage of non-interactive behaviors than did

adult males. Infants accounted for relatively few such behaviors.

Interactions between pairs of adult males were relatively frequent, as were interactions between mothers and infants, when compared to those between and within other age-sex classes. Interactions of adult females were relatively more evenly distributed (than were those of adult males) among other age-sex classes. However, juvenile and adult females interacted proportionately more with each other than with other classes.

Affinitive Interactions

Affinitive interactions were more frequent between pairs of same-sex partners for both adult and juveniles. Very strong relationships were found between adult males. Between juveniles and adults there also appeared to be a set of mutually affinitive relationships with members of the same sex. The strongest affinitive relationships were between adult and juvenile females. Preferences for same-sex partners were found in affinitive interactions between infants and juveniles.

Sitting Together

Adult males and females spent similar proportions of their time sitting with adults of the same sex. However, both adult males and females spent more time sitting with adult males than with adult females. In addition, mothers spent more time sitting with adult males than they did with adult females.

Juvenile and adult monkeys generally sat in sexually segregated groups or units: adult males spent significantly more time sitting with juvenile males than with juvenile females, who preferred to sit with adult females.

When the percentages of time which each age-sex class spent sitting with others was compared to that spent sitting alone, it was found that adult females spent proportionately more time sitting alone than did any other age-sex class.

Grooming

Adult spider monkeys showed no significant differences in their choices of grooming partners, in terms of adult male or adult female. In addition there was not a significant difference in the proportion of grooming bouts that adult males and females initiated and received. However, the trend for adult males and females to interact relatively more with adult males (seen in analysis of sitting together), was also a feature of the grooming patterns of adults. Adult males received proportionally more grooming from adult males and females than did adult females.

Adult females groomed adult males and other adult females in bouts similar in duration. However, mothers and juvenile females were groomed by adult females for significantly longer bouts than were juvenile or infant males.

Preferences for same-sex partners were found in grooming relations between adult and juveniles.

Agonistic Interactions

Agonistic interactions which involved direct 'altercations' or 'supplantations' within social groups were analyzed separately from longer distance agonistic behaviors, or 'confrontations' between groups (cf. Klein 1974, Cant 1976). It was found that, proportionately, adult males and females did not direct more agonism at partners of one sex than the other. However, adult males initiated relatively more and received less agonism than did adult females. Both adult males and females directed more agonistic behavior at adult females than at adult males. These encounters between adult males and females were frequently intimidating display chases by more than one adult male.

Between adults and juveniles, agonistic interactions were directed significantly more by adults, to juveniles of the same sex. Adult males initiated more agonism with juveniles than did adult females. Adult females directed agonism only toward juvenile females. It was found that the relationships between adults and juveniles of the same sex were stronger but multi-dimensional, incorporating both agonistic components and affinitive qualities, seen in their affinitive interactions, sitting together, and grooming interactions.

A comparison of the percentages of agonistic and affinitive interactions in adult male-female relationships, showed that adult females received proportionately more agonistic than affinitive behaviors from adult males.

Other Behaviors

Intergroup agonism, in the form of territorial or spacing displays, was performed by parties of adult males. Adult males also did more 'looking around' than did adult females. Threat-like behaviors directed at observers were recorded more frequently for adult females than for adult males. A vocal display, 'yelping' which appeared to signify periods of high tension in the monkeys, was performed more frequently by adult females than by adult males. In general, adult females were found to be more vocal than were adult males, despite the high frequency of contact calls between the latter. Adult males tended to exchange contact calls between themselves more than with others, indicating a more cohesive set of relationships among adult males. This suggestion is supported by the finding that adult males engaged in a specialized and ritualized greeting behavior called here the 'pectoral sniff and embrace'.

Play

Juvenile females in play with infant males accounted for the greatest total duration of play between and within age-sex classes. Infant males were focal in the network of play relations among juvenile males, juvenile females, and infant females. There was relatively little peer play between pairs of infant males and females, indicating that the sexual segregation between males and females at the juvenile stage is not necessarily a result of peer play.

Mother-Infant Interactions

Mothers spent more time engaged in care-taking

activities and affinitive activities (carry, eat in contact with, bridge for, sit with) with infant females, than with infant males. Only in grooming relations were infant males seen to receive proportionately more attention than did infant females.

In affinitive interactions with adults, infant females did not receive significantly different treatment than did infant males. However, relationships between juvenile and infants showed stronger affinity between same-sex individuals.

CHAPTER FIVE

DISCUSSION

The aim of this discussion is threefold. First, it focuses on the social relationships between and within male and female age classes in terms of the kind and amount of social interaction observed among individuals of these classes. Behavioral profiles of adult males and females are discussed with reference to these social relationships and certain actions of male and female spider monkeys at Tikal. Both the results detailed in the preceding section and pertinent anecdotal data collected by the researchers are used in this discussion. The findings of this study are placed in a comparative context. Their implications for some widespread generalizations about primate social behavior are discussed.

A second area for discussion is the development of the observed differences in adult male and female behavioral patterns, as these differences are revealed by the actions and interactions of juvenile and infant monkeys. Of interest are the interactions of adults and young male and female monkeys, as well as the general nature of actions and interactions of juvenile and infant monkeys with each other. Special attention is paid to the relationships between adults and infants which appear to set precedents for potential differences in male and female behavior (those differences noted between adult and juvenile spider monkeys).

Finally this discussion is addressed to the nature of the observed intra-group relationships and how they structure the social system of the population of Ateles geoffroyi at Tikal. Issues pertaining to both the kinds and degree of separation between male and female behavioral profiles are discussed. The emphasis is on how social tasks are performed by male and female spider monkeys, and how this distribution of tasks has shaped the observed organization of age-sex class relationships and associations.

Behavioral Profiles

Results showed that although there was considerable separation in the behaviors of adult male and female spider monkeys, the degree and nature of this separation varied according to specific relationships and actions in question. This discussion of behavioral profiles for adult males and females draws from the previous results, derived from analyses of these specific behaviors, to show how and how much the sex of the adult governed its participation in various activities (both interactions and non-interactive behaviors).

Adult Males

The most notable feature of adult male social behavior was the cohesiveness of social relationships between adult males. The strength of these bonds was revealed by the high proportions of affinitive interactions and sitting together recorded between adult males (Table

III, Table IV). In addition, relationships between adult males proved to be primarily affinitive, with relatively little occurrence of adult male agonistic behavior observed within the class (Figure 6).

The affinity characterizing adult male relationships with each other corresponds with a subjective impression obtained by the researchers during the course of the study, that adult males almost always travelled and foraged in unisex units. Males frequently moved into association with groups of mixed age-sex classes during times of play, rest, and for sleeping. Even at these times adult males tended to direct their attention, in the form of affinitive interactions, at other adult males, rather than toward other age-sex classes. When adult males associated with these mixed groups in contexts of rest, other age-sex classes (mothers, adult females) tended to focus their affinitive interactions (grooming, sitting with) on them. Indications of this pattern were present in the data on 'sitting together', a behavior observed during times of rest that requires a certain degree of 'tolerance' between the participants (Koyama 1973). Adult males spent the highest percentage of their sitting time sitting with adult males; as did adult females, mothers, juvenile males and infant males (Table IV).

When spider monkeys are foraging, it is very difficult to assess the nature of the relationships between individuals, or to tell which monkeys are in association

with each other. Proximity of one monkey to another is not necessarily a valid criterion for assessing these relationships, since distribution of the foraging monkeys is largely dependent on the dispersion of the food source being utilized (Klein 1972). Data from this study showed strong tendencies for adult males to sit together, indicative that there are distinct 'clumping' tendencies among adult male spider monkeys. This indicated that strong networks of relationships bind adult males together. Data from this study also showed that in a resting context, where adult males are clearly in association with mixed groups, relationships between adult males and other age-sex classes show mutual 'tolerance'.

The strong social bonds between adult males appeared to structure their association in small unisex groups during rapid locomotion, displays, and foraging. Evidence from the tabulation of 'affinitive' interactions showed strong cohesive relationships between adult males, but also between juvenile males (Table III). Included in this affinitive category were certain behaviors which occurred between monkeys moving together; i.e., follow, approach. Our field notes on the compositions of the male units, and the fact that juvenile males directed many affinitive interactions at adult males, suggested that adult male units often included juveniles moving in association with them.

However, the status of these juvenile males with the adult males, and within the social system in general,

appeared to be somewhat unstable (see section on development of sex differences: Discussion). Although juvenile males were frequently initiators and receivers of affinitive interactions with adult males, juvenile males were also on the receiving end of adult male agonistic behavior which was not reciprocated (Table VII). On many occasions juvenile males who had been chased by adult males, were seen to sit and whine for several minutes while the responsible male(s) moved off. Eventually the juvenile would follow, maintaining considerable distance between himself and the adult(s).

The high degree of cohesion and tolerance between adult males contrasts with the combination of agonistic and affinitive interactions which structured relationships between adult males and females. Hinde (1974) pointed out that social relationships involve many different types of behaviors, including agonistic interactions whose consequences might be construed as 'anti-social'. While adult male-male interactions within groups appeared to be affinitive in almost every case, male-female relationships were found to be less consistent, with relatively frequent agonistic behavior directed by males to females.

Affinitive interactions initiated by adult males toward adult females were fewer in number than agonistic interactions in which male(s) chased, displaced, or caused a female to retreat (Figure 6). Observations of similar incidents in Ateles groups were made in Colombia (Klein 1972; 1974) and in Tikal (Cant 1976). Klein (1974) noted

that while the onset of this sort of agonism involved rapid evasion, flight, and general symptoms of distress by the female recipients, hostility dissipated rapidly afterwards. He felt that almost all of these incidents were between members of the same social group, and that different relationships between the participants shaped the nature and outcome of encounters which occurred between them.

My description of male-female agonistic encounters concurred with Klein's observations (Klein 1974). Although the encounters appeared overtly aggressive to us, on no occasion did any of the individuals involved receive any injury. Most cases occurred when a group of mostly females was foraging or resting in an area. Typically a group of males, usually 2-3 adults passing through the area, would quicken their pace and move much more vigorously through the trees, with pilo-erection as they approached the mixed group. At this time this mixed association retreated, uttered distress barks, and cowered as the males directed their chase at one female (both females with and without infants were the recipients of these chases). The flight of the female being chased often ended 3-5 meters from the ground, where she remained until such time as the males moved off or continued their pursuit. The distress of females reacting to these intimidating displays of adult male aggression included loud distress shrieks, flight from the males, and conspicuously submissive postures. Both

events, the male approach and the female retreat, were so conspicuous in nature and repetitive in sequence that the researchers felt they were more ritualized intimidating displays than actual attempts by males to injure or 'chase away' the adult females, mothers with infants, or juveniles.

It was impossible to ascertain whether the same females who received the brunt of these chases were the same as those involved in affinitive interactions with the males responsible.

While these types of male-female interactions were observed almost daily, only two similar incidents in which an adult male was chased by other adult males were observed (once to the ground for several seconds, indicating that this was quite a severe chase).

Adult males also engaged in vigorous display encounters which were inter rather than intra-group. As described previously, a specific and stereotyped series of motor and vocal patterns characterized the behavior of adult males in these situations. Typically a small unit of adult males and occasionally juveniles, would position themselves near the top of a tall tree affording them a good view of the surrounding canopy, and look intently off in one direction. They exchanged loud howling cries with monkeys in the distance, periodically performing branch-shaking displays, leaping from branch to branch, occasionally mounting each other in the process. This display was seen frequently in various areas.

Our best documentation of these display encounters was made along the edge of the road into Tikal, where two separate groups of males could be watched simultaneously exchanging these display behaviors. Because this road made a complete break in the canopy (wide enough to defy arboreal crossings by spider monkeys) for several kilometers into Tikal, we were reasonably sure that these were separate troops of spider monkeys. Although females were often in the area as the males fanned out to perform these displays on opposite sides of the road, they were never seen to take part in the actual display behaviors. These displays correspond in nature to territorial 'confrontations' described by Klein (1974).

Apparently analogous male displays were described in Section II, for several other species of monkeys: colobus monkeys in Uganda (Marler 1969), Nilgiri langurs (Poirier 1969), vervet monkeys (Gartlan 1968, Struhsaker 1969). The description of the display performed by adult male langurs could be applied equally well to that of male spider monkeys:

> The display was differentiated into two components; the whoop vocalization and the bounding about through the trees. Displaying males jumped about between branches and trees in a taut heavy manner, producing a noisy clamor. Branches often broke under their weight and came crashing to the ground. The objective appeared to be to create as much noise as possible. (Poirier 1968: 33)

Eisenberg *et al*. (1972) suggested that the role of adult males in multimale social systems includes the maintenance

of spacing with respect to neighboring troops. It seems likely that forms of male displays described here for spider monkeys could function for spacing of these troops and/or general definition of territories.

Eisenberg et al. (1972) made mention of other tasks commonly performed by adult males in multimale systems. One of these is driving out younger males to reduce competition. Little evidence was found that the adult male spider monkeys at Tikal ever attempted to drive out young males. Juvenile males received both agonistic and affinitive behaviors from adult males. These actions were seen more as evidence that at the juvenile stage males are in the process of shifting the focus of their social relationships away from the natal group, and developing associations with adult males (see section V: Development of Behavioral Profiles, for further discussion). The frequency with which adult and juvenile males were seen in association with each other indicated that unisexual male units may be age-graded. Eisenberg (1976) pointed out that the social organization of spider monkeys may hinge on these age-graded, closely related male units; and therefore not conform to the traditional classification of multimale units.

A second proposed task of adult males is to enforce some degree of protection against predators (Eisenberg et al. 1972). At Tikal predator pressure did not appear to be a particularly strong factor shaping the behavior of adult males. (This fact is discussed further in the section

dealing with adult females). Although there was no direct evidence to this effect, according to local sources it is possible that feline predators, birds of prey, and possibly arboreal snakes were potential dangers to the spider monkeys (especially young monkeys). The role of troop 'protector' involved many aspects of behavior, and the motivation behind a territorial display may not be the same as that involved in initiating troop flight from a disturbance or performing a threat to a predator. There are no direct data here which substantiated the premise that males were more responsive and/or defensive to these potential dangers, while there were indications to the contrary (section on role of adult female). Gartlan's work with vervets showed how the males performed territorial displays and also social vigilance activities in the form of 'looking out'. These activities are consistent with patterns in male spider monkeys at Tikal.

Another recurrent theme in the literature is expressed by Mitchell and Tokunaga (1976) in their treatise of sex differences in primate grooming, to the effect that adult females generally groom more than do adult males. Chalmers (1972) suggested that in five species of Old World primates, adult males receive less affinitive grooming and aggression. In spider monkeys, the two traits found by Chalmers for these Old World species do not go hand in hand with each other. While there were significant differences in the amount of agonistic behavior adult males and

females received and initiated (less was received by adult males, Figure 5), adult males did not initiate or receive less grooming than did adult females (Table V). Like other affinitive interactions, adult males received more grooming from other males and from females than did adult females.

Grooming in spider monkeys only occurred in relaxed resting periods, usually when individuals were clumped together in what appeared to be 'familial' groups. It may be that grooming between adult male spider monkeys is more prevalent between related individuals, and the preferences are not on the basis of sex as much as they reflect kinship ties.

One adult male who was identifiable to the researchers by a large stomach tumor, was often seen in association with a particular mother and infant male, also recognizable by her constant association with a very emaciated juvenile female with a broken arm. When he was in association with these monkeys, the adult male sat with these three individuals and exchanged grooming with the adult female (mother). However, he was seen more frequently in association with several other adult males, also recognizable to the researchers because one had a broken arm and another had a very light colored coat. At these times he engaged in affinitive interactions with them, and was involved in agonistic encounters with adult females.

Because there was no way of ascertaining kinship

beyond that between mothers and infants, it remains to be seen whether indeed such associations as this adult male, adult female, and her young which groomed and sat together, were 'familial'. If it is true that these associations of adult females and adult males in relaxed activities involved closely related individuals, it follows that male behaviors at these times are distinct from those when they are in rapidly locomoting or displaying groups of adult males.

In addition, affinitive relations within adult male units appeared to permit a great deal of co-operation between individuals in their activities, without frequent or conspicuous displays of dominance or agonism within the groups. It is likely that Eisenberg was correct in speculating that these all-male groups strongly reflect kinship ties, in addition to a mutual tolerance which develops through continually renewed contact through the years (Eisenberg 1976).

It is possible that the activity patterns of the adult males, and their ability to change associations from mixed to all-male groups with appropriate changes in behavior, demand special sets of communicative gestures which facilitate these transitions. The 'pectoral sniff and embrace' is a form of greeting which involved specialized motor patterns, and whinny vocalizations are used almost exclusively by adult males approaching or meeting each other in a tree. It seems possible that this gesture, which involves a mutual embrace and possibly an exchange of olfactory cues

(Klein 1972), may have been a means of renewing contact between males. The loose grouping patterns of monkeys during the day in foraging, necessitate modes of communicating other than visual cues, which are of limited use in an arboreal habitat. The prevalence of contact calls exchanged between adult males may also substantiate the suggestion that male networks maintain some cohesion, despite frequent maneuvering in and out of mixed associations (Table IX).

The appearance of units of adult males travelling, foraging, and interacting together does not preclude the occurrence of a variety of male interactions with other age-sex classes. In general, adult males both initiated and received many affinitive actions, relative to the numbers of agonistic interactions in which they participated (Figure 6). This pattern is in contrast to the situation portrayed for many other primate species, including those whose social organization appears superficially very similar to that of spider monkeys. Saimiri sciureus is an arboreal New World species which lives in large multimale-multifemale groups (Baldwin 1968, 1969, 1971; Coe and Rosenblum 1974). As in Ateles, adult male squirrel monkey units travel around, and apart from larger female associations (Coe and Rosenblum 1974). However, differences between Ateles and Saimiri social groups appear when the relationships within the groups are examined. Baldwin (1968, 1969, 1971) found that relationships between adult male squirrel

monkeys were primarily agonistic, and hierarchically structured. In contrast, adult females were social unifiers to whom most of the affinitive interactions were directed. In a review of male roles in primates, Redican (1976) suggested that in primates where there is multimale organization, adult males seldom engage in prolonged affinitive interactions.

This study has shown that there was cohesion and cooperation within adult male units. The qualities of affinity and agonism were both prevalent in the relationships of adult males with adult females, juvenile males, and mothers with infants. This description of strong relationships within the larger multimale-multifemale social system raises the question of how such social organization should be described and perceived.

> ... schemes for classifying the group structures of non-human primates are of only limited usefulness: more detailed analyses of group structure in terms of interactions between members are urgently needed. (Hinde 1974: 325)

The nebulous multimale classification and generalizations for behaviors within such a system may not be applicable to the social organization of spider monkeys, without some refinement at the level of interactions and actions of the individual components. When this analysis was performed for spider monkeys, it was found that relationships were very affinitive between adult males within the local population, where competition between males might be expected to be high (Cant 1976).

Eisenberg's (1976) suggestion that Ateles social organization is one with multimale units which are age-graded groups of related monkeys, may explain the high cohesion between males noted here. However, the co-operation of up to 12 fully adult males in intertroop displays indicates that kinship can only in part explain the consistent lack of agonism between all the adult males in this localized population of spider monkeys. It appeared that continuous association with other juvenile males during socialization periods, and later with other adult males, permitted the formation and maintenance of primarily affinitive bonds within adult male units of this population of monkeys.

Adult Females

The behavior of 'adult females' was analyzed, and is discussed separately from that of 'mothers' or adult females carrying dependent infants. The purpose here is to ascertain how female behavior differs from that of adult male spider monkeys in ways other than those connected directly with nurturing young infants. While females were usually in association with young, probably their own offspring, their daily activities of foraging and locomoting are not shaped by the presence of the young as strongly as are those of a mother who must provide for the needs of an infant who cannot eat or move independently. Because female spider monkeys are the primary caretakers of the young, their role involves daily activities which are structured to some extent to suit the needs of the young. Females with young

are said to associate with other females and young of similar ages, permitting formation of play groups among peers (Cant 1976). Eisenberg also pointed out that the mobility of females who are encumbered with young (both mothers carrying infants and those females travelling with very young juveniles unskilled at negotiating the arboreal pathways) is reduced somewhat. He said that this lack of mobility may in part account for the formation of small female subunits (Eisenberg 1976: 68).

The behavioral differences between adult males and adult females which are analyzed in this discussion are felt to reflect a fundamental divergence in the respective socialization of the sexes. These differences are attributable not just to the essential biological requirements of being a mother, but also to the basic ways that adult female behaviors are shaped around, and accomodate these maternal demands. Of interest are threat responses to danger, alarm calls, and many kinds of interactions with other troop members, choice of a sexual partner, and subgroups which are formed in the course of daily rounds. While adult male spider monkeys showed very strong affinities within their own age-sex class, the affinitive interactions of adult females were distributed more among individuals of each age-sex class (Table III). Adult females directed a higher proportion of affinitive behaviors than agonistic behaviors to adult males and females (Figure 6). Some preferences for partners of the same sex in affinitive interactions did

indicate the presence of a certain degree of sexual segregation between adult males and females.

The wider network of female relationships with other age-sex classes coupled with a strong emphasis on affinitive relationships between adult and juvenile females, presents a different picture from that drawn for adult male social relations. Cohesion between adult and juvenile females was stronger than that found between adult females. A disproportionately high frequency of affinitive interactions was exchanged between adult and juvenile females (Table III), while very few agonistic encounters occurred. Adult females groomed juvenile females in longer bouts, and more frequently than they did any other class. Similarly 'tolerance', measured by amounts of sitting together, was found to be greater between adult and juvenile females than it was between adult females (Table IV).

In addition, 'tolerance' of adult females for adult males was found to be greater than expected, given previous results showing male aggression to females and the suggestion that in many other species, 'tolerance' is greatest within sex classes (Koyama 1973, Baldwin 1968, 1969, 1971; Simonds 1974). Adult females sat with adult males more than they did with other adult females (Table IV). There was no evidence that adult males and females preferred to groom members of their own sex over adults of the opposite sex (Table V).

As discussed previously (Discussion of adult male

behavioral profile) grooming between the sexes may have been between closely related males and females. In the general pattern of male-female interactions, the relationships between adult males and females were not found to be strongly affinitive, or uniformly agonistic. Adult females initiated and were receivers of high frequencies of affinitive interactions with adult males, but they received more agonism from adult males than they initiated with adult males (Figure 6). There is no evidence that there is a breeding season in Ateles (Klein 1972). Therefore it seems unlikely that adult male-female relationships are subject to significant effects attributable to hormonal or behavioral changes which offset yearlong relations during breeding seasons in other species. Baldwin (1971) reported that in squirrel monkeys, where strong affinitive relationships are periodically formed between adult males and females, adult females were primarily recipients rather than initiators of 'friendly' interactions with adult males and females. He said that other adult female relations are inconspicuous. In contrast, adult male spider monkeys have been shown to direct a great deal of agonism, in the form of intimidating displays and chases, at adult females. Secondly, relationships between juvenile females and adult females are conspicuously affinitive in nature.

Despite the fact that adult females generally locomoted in associations comprised of other adult females, juveniles, and mothers with infants, it seemed that in the

course of foraging activities these groups further subdivided or dispersed. Units containing one adult female and just one juvenile, or adult females well separated from others, were frequently encountered. Cant (1976) commented that adult females were 'solitary' more often than expected. Although we also had the impression that adult females were often well separated from others, or 'solitary', it was likely that they were rarely out of vocal contact with other females. It was found that adult females were much more vocal than were adult males, when frequency of all types of vocalizations were taken into account (Table VIII). In addition, adult females spent more time sitting alone, relative to that they spent sitting with others, than did any other age-sex class (Figure 3).

The periodic dispersion of the large female associations during foraging was attributed to the constraints of a frugivorous diet, necessitating use of widely dispersed fruit trees. Assessing the degree to which these small foraging units of adult females and juveniles, or females with infants, or females along, are 'solitary' is perhaps of less value than recognizing the ability of females to disperse widely to forage, and to re-unite in large sleeping associations of mixed age-sex classes during times of locomotion, rest, and sleeping.

After initial movement of associations of females, juveniles, and infants out of the central sleeping areas just after sunrise, it was usual for individuals to fan out,

alternately feeding and resting in small units. This behavior corresponds to Bramblett's (1976) description of the activity patterns of spider monkeys at Tikal. It was also common for these associations to re-unite periodically through the day. At these times, adult males, adult females, and mothers were commonly seen in close proximity; while juveniles and infants congregated in large play groups. Eisenberg (1976) noted that subgroups of females are found not only on the basis of long term affiliations between females, but also because of developing relationships (usually through play interactions) with peer groups. It seems safe to assume that this is true for spider monkeys, where young of all ages benefit from associations with individuals of similar ages and sexes. The formation of play groups enabled juveniles and infants to interact not only with each other, but also gave them an opportunity to interact with adult males who often joined the larger associations and engaged in play (Table VI), or sat with mothers of the infants and juveniles who were engaged in play (Table IV).

In the preceding section it was noted that adult males engaged in territorial displays with neighboring troops. However, there were not grounds for assuming that this behavior was representative of a wider male role as troop protector. While adult females did not actually perform howl behaviors, it was not uncommon for them to make loud howling vocalizations (reminiscent of yelps) during

the male displays. The results of the study indicated that 'troop defense' is a concept which involves a complicated and diverse set of behaviors which are divided between the sexes.

Adult females responded with more threat-like behaviors to potential danger than did adult male spider monkeys at Tikal. Branch-shaking threats (usually directed at human observers) were used more frequently by adult females than by adult males, who acted somewhat less concerned by our presence than did adult females. In addition to their responsiveness to terrestrial intruders, the females appeared to play an instrumental part in prolonging and initiating 'yelp' sessions, which were interpreted as a form of alarm calling. During 'yelp' sessions, loud repetitive barking sounds contrast the longer high-pitched howls given by adult males during their intergroup displays and calls, and the monkeys remain virtually immobile in a tree. Several individuals could be involved in these yelp calls, including adults and juveniles of both sexes (Table VIII); but adult females were most conspicuous in these sessions. Often the calls would trigger simultaneous bouts of yelping in nearby subgroups.

Although yelping usually occurred in subgroups composed of females and young, it seemed that it was initially the response of one individual who became aware of some source of danger or disruption. We observed and heard these calls late in the afternoon when subgroups were

shifting about in the central area of the park in preparation for evening sleeping. In addition to their own movements at this time, there was also a general movement of people out of the park along the paths, a disturbance which may have served to arouse the monkeys.

On one occasion we were able to locate an adult male and female by their yelping, which could be heard from a distance of several hundred meters. When we caught sight of these individuals, they were sitting on an unusually low tree-limb, staring intently into a section of dense vegetation on the ground below them, uttering yelps. Although we were unable to locate the source of their concern, it was possible that they had seen a snake or cat in the area. Cant (1976) reported that at night, spider monkeys reacted to his presence with a special whining call, which he interpreted as a response to predators. Early accounts of yelping as a response to predators (black and white eagles) are cited in Forbes (1896). Klein (1974) suggested that the tayra (Eira barbara) was a potential predator for Ateles belzebuth in Colombia, and these animals were also present at Tikal. At other times when we located and followed solitary individuals who were yelping (usually adult females), we felt that the call may have been a general distress or 'lost' call.

Distinction has been made between various forms of agonism. Yelping and other loud calls which may serve to space groups are viewed separately from the territorial

male display howl which involved similar howling and yelping in association with vigorous leaping in branches, embracing other adult males, and branch shaking. This behavior in turn is discussed independently from branch-shaking which may in fact occur in territorial displays. The distinction between these behaviors is not as clear in terms of motor patterns and vocalizations used, as it is in terms of the context in which they are seen.

Klein (1974) pointed out that various forms of agonistic interactions between conspecifics involved behaviors similar in nature or form to those elicited by potential predators in Ateles belzebuth in Colombia. He said that responses such as branch-shaking, common in some arboreal primates, may be due to varying causes such as terrestrial observers, and high degrees of social tension (Klein 1974). He suggested that:

> ... they may be interpretable as either generalized and/or ritualized expression of an immediately instrumental aggressive act, particularly likely to be performed by those arboreal animals for whom balance and agility must play as important a role as strength and speed in determining relative fighting ability. (Klein 1974: 86)

This discussion has revealed that there are tendencies for male and female spider monkeys to utilize different forms of agonism for apparently different purposes. These 'purposes' are in turn reflected by the behavioral profiles of adult male and female monkeys. Cohesive relationships between adult males are both promoted by, and also permit cooperation in associations of males performing intragroup and intergroup

displays. However, male participation in forms of agonism such as might be elicited by predators, was clearly no more and possibly not as important as that of females.

The vigorous response of females to 'potential sources of danger' (meaning human presence, possible predators, and periods of high tension in the group) contradicts the premise that female primates have a passive nature, as mentioned previously by Harlow and Lauersdorf (1974). Our results are in accordance with those from other studies of feral monkeys. As detailed by Struhsaker (1969), in Cercopithecus monkeys, adult females perform alarm calls and retreat responses, distinct from the loud display calls given by adult males which function to maintain group cohesion and intergroup spacing. Similar responsiveness of adult females to a disturbance (especially human) was noted by Candland et al. (1973) in squirrel monkeys.

In summary, then, adult females maintained a broad network of associative relationships with all other age-sex classes, as well as a very strong set of cohesive bonds with juvenile females. It was inferred from fewer affinitive interactions between adult females and juvenile males, that the juvenile male is less attached to the natal group and female associations (Table III, see section V, on the development of behavioral profiles, for further discussion). Adult females with and without infants were able to move off from these associations to forage; but reunited in large congregations for periods of locomotion, rest, and sleep.

It was not surprising that female spider monkeys were at least as responsive to external intrusions as were adult males, given their usual pattern of association with their own offspring and/or females with offspring (Jay 1964, Baldwin 1968, 1969, 1971; Gartlan 1966; Lancaster 1973, 1976; Simonds 1974). Matrilineal associations have been reported to structure groups of Ateles in previous studies (Rondinelli and Klein 1975: Eisenberg 1976, Cant 1976).

Development of Behavioral Profiles

The preceding discussion showed that sex differences exist between adult spider monkeys in their interactions, and associations not only with each other, but also with young monkeys. This section focuses on the latter, and looks at ways in which the behavioral profiles of young male and female juveniles differ. Sexual segregation in associative patterns of adults was much less clearly defined during times when monkeys were sitting together and grooming. However, in all forms of interactions (except play), sexual segregation strongly characterized bonds between juveniles, and between juveniles and adults. Results showed that juvenile males and females seldom interacted with each other, in affinitive or agonistic interactions (Table III, Table VII). This lack of interaction may reflect an increasing separation in association patterns of male and female juveniles, and a concomitant development of behavioral profiles appropriate for adult males and females. Jensen

et al. (1967) suggested that differences between young male and female monkeys are usually parallel in nature, if not in degree, to those of adults.

Juvenile males appeared to be making a transition in the focus of their social interactions. They initiated more affinitive interactions with adult males than they did with adult females. In addition, juvenile males were recipients of more affinitive and agonistic interactions from adult males than were juvenile females (Table III, Table VII). Juvenile males spent more time sitting with others than they spent sitting alone, and most of this time was with adult males (Figure 3, Table IV). These interactions are indicative of developing but unstable relationships between adult males and juvenile males. These relationships are seen as part of the shift in the association of juvenile male, from female to male units.

The detachment of juvenile male rhesus monkeys from their natal groups results in the formation of groups of young males who remain peripheral to the larger association as they gradually establish ties with new group members (Drickamer and Vessey 1973). At Tikal, although units of two juvenile male spider monkeys were occasionally seen travelling together, there was no evidence that juveniles were peripheral to other monkeys. Their interactions with adult males was frequent, not indicative of avoidance behavior characteristic of pheripheral males.

Eisenberg (1976: 68) noted a tendency for adult

male spider monkeys to actively seek out and affiliate with younger males in the formation of age-graded male subunits. In this study it was shown that juvenile males initiated more affinitive interactions with adult males than they received, suggesting that it was the juvenile who sought to establish relationships with adult males (Table III, Table VII); while adult males did remain apparently tolerant of juvenile males during this interaction. It is possible that this tolerance reflects kinship ties between the males (Eisenberg 1976), and earlier affinitive bonds during association with the mother. Eisenberg (1976) also suggested that if juvenile males cannot form affiliations with older males (captive settings), they may be severely persecuted.

The juvenile period for females involved close association with adult females and continuation of early cohesive relationships within female groups which persist into adulthood. Relationships between adult and juvenile females were very cohesive, given evidence from all kinds of affinitive interactions including grooming and sitting together. Juvenile females spent more time sitting alone than they did sitting together, unlike juvenile males; but similar to adult females (Figure 3). Because associations of females likely reflected kinship ties (Lancaster 1973, 1976) and stable affinitive networks of relationships, both adults and juveniles were able to maintain a certain degree of independence in the course of their daily foraging activities.

These patterns agree with suggestions made by Jensen et al. (1967) and Gartlan (1968) in the discussion of sex differences and their development. Juvenile males generally appeared to make a transition in the focus of their social interactions from female to male bonds; while the juvenile period for females involves close association with adult females, and continuation of relationships with females which last through their lives.

In a description of ontogeny in squirrel monkeys, Baldwin (1969, 1971) found that differences in behavior between adult males and females could be traced back through the juvenile and infant periods. Juvenile and infant play is generally felt to be one of our best tools for looking at the development of these sex differences (Baldwin 1969, 1971; Simonds 1974).

A pattern in some other primate species shows that juvenile males engage in more rough and tumble play than do females, who engage more in forms of interaction such as grooming (Sade 1965, Simonds 1974). Results of this study show different patterns in spider monkey play. First, duration of play recorded for juvenile females was relatively greater than it was for juvenile males. Secondly, there was not any apparent qualitative difference in the roughness of the play of juvenile males and females. Both sexes played primarily by 'grappling'. As described in the ethogram, grappling might be seen as an arboreal analogue to play wrestling in which as many as five individuals hang from their tails, engage all four limbs in pushing

and kicking each other, playbite and emit a cough-like type of play vocalization. This vigorous play was very common between juvenile males and females, and among juvenile females; while it was relatively infrequent between juvenile males.

These results suggest that grappling was not a 'dominance' activity utilized by juvenile males to establish their status with other males, as suggested by Eisenberg and Kuehn (1966). Instead it is a boisterous form of play which provides juveniles and infants of both sexes with opportunities to interact with their peers. The sexual segregation which characterizes the affinitive networks of young spider monkeys is crosscut to some extent by the play relations between juveniles and infants. Play between juvenile females and infant males accounted for the highest percentage of play time, while play between infant and juvenile females was considerably less time-consuming. There was little interference by adults, either male or female, in these play interactions although they occasionally became involved in brief bouts of play if approached by a playful infant or juvenile.

The different emphasis of male and female play (juvenile males did not show as strong a tendency to interact with many other age-sex classes as did juvenile females) may be a reflection of the fact that juvenile males and females engage in different sets of social relationships. Peer relations among juveniles are pre-

sumably integral in the development of later adult social networks. It has been seen that males and females have different patterns in associations, and it is likely that they are subject to different sorts of socializing influences.

Furthermore, it is probable that the socialization of juvenile males and females involves relatively independent processes and that they may differ in rate in their effects on young monkeys. The play of infant males with juvenile females, and the relative lack of play between infants, indicates perhaps that male and female infants were at different stages of social and physical development. Because infant males focussed their play interactions on juvenile females more than infant females (Table XI), it may be that this pattern indicates an earlier expansion of social relations and independence from the mother in infant males than females. This point is best illustrated in Figure 7, where it is shown that infant males were focal in the network of play relations.

Other studies of macaques have shown that relations between young males and their mothers result in greater and earlier independence of infant males (Jensen et al. 1967). In this study, differences in mother-infant relations for male and female infants were found to support this observation. Mothers permitted greater and perhaps longer dependence of infant females than males. In addition infant females spent more time sitting in contact

with mothers than did infant males. This contact may be initiated mutually by the mother and infant, indicative of more permissiveness on the part of the mother, and/or greater dependence of the infant females. Thus there are apparent differences in the interactions between male and female monkeys at both the infant and juvenile level. It should be stressed, at this point, that these are only crude indications of very complex and subtle differences in the socialization of young male and female spider monkeys.

In addition to infant relations with mothers and peers, some possible influences of adult males merit consideration in a discussion of socialization of young monkeys. Adult male units were frequently present at times when large associations of females congregated, and play between young monkeys occurred. Mothers were seen sitting with adult males frequently, and these occurrences were usually in such a context.

There was a lack of overt affinitive interaction directed by adult males towards either male or female infants. However, infant males initiated a considerable number of affinitive actions with adult males, noticeably more than did either infant or juvenile females (Table III). It is notable that the expansion of infant male relationships involved interactions with adult and juvenile males (Table III, Figure 1). These interactions with infant males involved a minimum amount of overt participation on the

part of the adult males. Nevertheless, the fact that there was little agonism by adult males towards infant males indicates an attitude of tolerance by the adult male for infants.

On several occasions when adult males and mothers with infants were seen in association, mothers moved off slightly, leaving males and infants together in a tree for periods of up to 60 minutes. Resting males were frequently approached by infants (males more than females, Table III), who usually spent several minutes crawling on, play-biting, and embracing apparently unconcerned adult males.

On one occasion an adult male was observed carrying and bridging for an infant male. At the time the mother of the infant had separated from him to forage, and the infant approached and followed an adult male associated with the mother-infant dyad. When the adult crossed a particularly difficult gap between two trees, he stopped and bridged for the crossing infant. The infant had begun to whine; and instead of crossing the 'bridge', he climbed onto the back of the waiting male, and was carried for several seconds by him.

The high tolerance of adult males for infant contact at these times is in sharp contrast to the chases which adult male groups were seen to direct on occasion, at adult females with and without infants. It is possible that both of these aspects of adult male relationships were

influential in the socialization of young monkeys. It also seems likely that the developing bonds between adult and juvenile males may have their roots in interactions which were seen to occur between adult males and infant males.

Discussion and Conclusions: Social Behavior and Social Organization of Spider Monkeys at Tikal

At this point the focus of the discussion shifts somewhat, to some general patterns in the social organization of spider monkeys. Moving from the level of intragroup structure, the social relationships between and within age-sex classes are discussed as dynamic components of the social structure of Ateles (Hinde 1976). Ecological parameters as external structuring devices of social behavior are also considered. An attempt is made to integrate results from causal types of questions asked in this study, with the socio-ecological findings of studies employing a more functional approach to the social behavior of Ateles (Carpenter 1935; Klein 1972).

Klein (1972) suggested that seasonality of fruiting trees figures prominently in shaping the activity patterns and the social grouping of spider monkeys. He noted that fluctuations in dispersion and size of subgroups were highly dependent on the fruit availability in an area. In accordance with his suggestion, our field notes show that when foraging in various trees with differing abundance, dispersion, and size of fruit, spider monkeys exhibited different

spacing patterns, both within trees and within an entire area. While some shifts in foraging strategies apparently resulted from shifts in availability of major fruit sources, the basic activity patterns and group characteristics did not apparently undergo major changes. Although we found that arboreal pathways, sleeping areas, and group dispersion were subject to periodic (and for us, unpredictable) variation, there is evidence that there is also consistency in these over time. Bramblett's (1976) team marked arboreal pathways being used by the monkeys in the wet season (July-August) of 1972. In the dry season (December-May) of 1968, we found that these paths were still in periodic use, substantiating the belief that the monkeys have well-defined ranges and patterns for habitat utilization. Staggered seasonality of fruit sources and the variety of food sources utilized by Ateles, mean that at any time of the year, food is likely available on any of the arboreal routes being utilized by the monkeys.

While group activities and daily rounds were shaped by the seasonal availability of fruit in certain areas, other factors merit consideration. By the end of our study, we were able to recognize several monkeys, and consistent associations between these individuals. Records of the observations of these monkeys and the routes over which they were followed, indicated that each day or every few days, the direction of their day's travel changes. These transitions were too rapid and brief to be accounted for

only by the seasonality of ripe fruit along the routes. Alternation of routes from day to day indicated that the relation between group movements and seasonality of fruit is very complex. Other variables such as inter-troop spacing and the extent to which fruit in the area had been depleted by previous foraging of monkeys were felt to be responsible, in part, for these patterns.

While the ability of the spider monkey troops to fuse and fission has been seen as a reflection of ecological determinants, the limits of this flexibility are also dependent on the stable components of the troop; i.e., the behavioral profiles of individuals within the social system. It is most useful to look at foraging behavior as the product of an interaction between ecological and social elements. The flexibility which we observed in habitat utilization appeared to be built in to the social system of the monkeys, within which consistent social patterns and structure could be discerned. Hinde (1976) referred to this quality of social structures as one of 'dynamic stability'.

For illustration of this interaction between ecological and social factors, events during one week in April when a particularly large (and fortunately, easily observed) Ceiba tree was in full fruit, are described. The large size of this tree crown, and the abundant and wide distribution of fruit throughout the tree, permitted as many as thirty monkeys to forage in it simultaneously, which they did for periods of several hours at a time.

This particular tree was located in an area frequently used for sleeping. Both prior to, and during fruiting, the tree was used for sleeping by monkeys.

For one week when the tree was in peak fruit, about thirty individuals of all age-sex classes were seen to congregate in it at approximately 1500 h. each afternoon until dusk. They also remained foraging, playing, sleeping in the tree for two hours after dawn each morning before moving out of the area for daily activities. These periods in this large tree involved prolonged and intensive play sessions among as many as ten juveniles and up to seven infants of both sexes. Adult males and females occasionally joined in this play, or sat with and engaged in grooming with the young. Generally, however, the adults foraged alone or in the vicinity of the tree, or sat apart from the play in mixed groups of adult monkeys.

Of interest is the fact that as groups congregated in the tree in the afternoon or moved out in the morning, they did so in smaller units whose age-sex compositions were well-defined and easily recorded by the researchers. At these times groups of three or four adult males (often in association with one or two juvenile males) were consistently seen moving together, a pattern which is in keeping with the patterns of affinitive relations between adult males noted in this study. In addition there was reason to believe that these male sub-units did not sleep with the larger mixed age-sex associations in this tree. They were

often observed moving into the tree at dawn, from nearby trees. Young were frequently already playing there, and other males, females, and mothers of offspring were sleeping or foraging. The arrivals of male subunits in this Ceiba tree were frequently accompanied by brief agonistic interactions. However, there is no evidence that the males intended to chase females out of the area; since both male and female individuals were seen to remain in the tree or in the immediate area, following these incidents.

When the females and young moved in and out of an area, it was common for their associations to consist of several adult females, juveniles, and infants with mothers. When followed along an arboreal pathway, these associations usually dispersed until relatively independent subunits composed of just one or two females with young were being observed. This pattern corresponds with Cant's (1976) observations at Tikal and Klein's (1972) report of mean group size in Colombia. However, as described previously in this study and noted by Coelho et al. (1976), these female associations apparently maintained vocal contact with each other; and it was not uncommon to find them reuniting in an area for resting together, playing and relaxed foraging in the course of their daily rounds through the forest. On several occasions small subunits of males or females were followed, and they eventually led the researchers to an area where larger mixed associations were congregating or already present.

What might have appeared to us as a confusing and disorganized process of aggregation and dispersion of mostly unidentified monkeys, seemed to be, in fact, a regular and systematic behavior pattern familiar to the monkeys. Coelho et al. (1976) described daily circular migrations of units of spider monkeys in fragmenting and non-fragmenting groups which exhibited compact or dispersed spacing. They noted that large units composed of individuals of all age-sex classes often subdivided into smaller, more homogeneous units: adult males, various combinations of adult females with juveniles, and mothers with infants. In fact it seems that any one individual is capable of exhibiting any or all of these grouping patterns through the day, in the course of their daily rounds. This fact explains, perhaps, why researchers have been unable to define permanent or stable groups of spider monkeys. The smaller units of two or three individuals in association may reflect very strong bonds or kinship ties between their component members (Eisenberg 1976).

Typical compositions of these smallest foraging units were adult with juvenile female, two or three adult males (often in association with juvenile males), or mothers with infants and/or juveniles. Both field notes taken on group compositions, and very strong affinitive bonds found to exist between these age-sex classes, point to these small social units as basic structuring units within the social system. As shown by the activities in the Ceiba tree,

at some times the activities of the spider monkeys resulted in the congregation of individuals in larger associations: sleeping, territorial displays, and foraging in large trees with abundant ripe fruit. The larger looser networks of relationships between the monkeys which permit this flexible and periodic aggregation, also may be reinforced at these times. Sexual segregation which characterized smaller associations of adults and juveniles is cross-cut somewhat in larger ones. Adult males and adult females (mothers included) sit together and engage in play. Young monkeys are able to engage in vigorous play with peers, and expand their own networks of social relationships beyond their natal groups at these times.

Sugiyama's (1969) description of chimpanzee group movements and social bonds in Budongo forest correspond in many ways to this, and previous studies of spider monkeys. Cant (1976) also commented on the similarity between social organization of Ateles geoffroyi and that of Pan troglodytes. Descriptions of 'regional populations' of identifiable chimpanzees have shown that in addition to age-sex classes, kinship is also important in the organization and maintenance of troop activity (cf. Reynolds 1963: Goodall 1965). Sugiyama (1969) pointed out that within a 'regional population' of about 50 individuals there was no rigid dominance ranking of individuals. He described strong bonding between adult males which was maintained by friendly or associative interactions, while females were less prone to

gather in such parties. Sugiyama (1969) also noted that temporary parties formed and scattered throughout the day, similar to patterns described for Ateles.

In addition, Sugiyama commented on the outbursts of 'booming' vocalizations that apparently communicated the existence of good fruit to members of the population and indicated the relative positions of individuals to each other. Like that of chimpanzees, spider monkey social organization appeared to be structured primarily around networks of loose relationships between and within age-sex classes, and it seemed likely that kinship ties were responsible for many of the associative tendencies noted for the monkeys in this study. A complex communicative system, involving both specialized vocalizations and olfactory cues, permitted much flexibility in associative patterns exhibited by the monkeys as they moved through their daily activities.

There was no evidence that the spider monkeys had a distinct ranked hierarchy of either adult males or females, as frequently described for other primates (i.e., macaques, baboons, squirrel monkeys). It is possible that the high frequency and the repetitive nature of male agonism towards female monkeys represents some form of dominance assertion. Such behavior was exercised most often by adult males in units of two or three, acting in coalition as they moved through an area where female associations were located. Further observations of such encounters, and identification

of the individuals involved would be required before interpretation of these encounters would be justified.

Affinity between adult male spider monkeys appeared to permit their co-operation with each other in both offensive displays and the defensive forms of territorial displays between troops. Male co-operation has been documented by other researchers dealing with spider monkeys (Klein 1972; Eisenberg 1976; Cant 1976). In the Ateles population at Tikal there was flexibility in the use of arboreal pathways by the monkeys from day to day. Groups of adult males spent much time, and apparently much energy in displays which may have defined territories and home ranges of their respective troops. These may have served to prevent encroachment on the territories of one troop by contiguous populations. Thus it is possible that the observed associations of males were not only units formed for foraging purposes, but that they incorporated movements into their daily rounds which took them to strategic areas for the exchange of vocal and/or visual displays with males of neighboring troops.

Both male and female spider monkeys emit very loud calls through the day, especially just prior to rapid group movements at dawn and in late afternoon. Answering calls could often be heard at these times. Thus the monkeys may have been aware of the spacing of neighboring troops before they began their daily movements. During the day, occasional outbursts of similar calls occurred, and these may have served to maintain inter-troop spacing and the distribution

of monkeys of one troop within a local area. Similar spacing has been noted for other arboreal monkeys and chimpanzees (Chalmers 1973; Sugiyama 1969).

In this study a rudimentary attempt to integrate the causal and functional approach to social behavior was made, by bringing information about the social relationships between individual monkeys to bear, in drawing a picture of the broader workings of the social system of spider monkeys at Tikal.

Without moving beyond the limits of the data collected in this study, it is not possible to make any further or more conclusive statements about how or how much the daily activity patterns of spider monkeys reflect the internal structuring of their social groups. Such discussion must await a much longer study in which intensive efforts are made to recognize individuals who may then be assigned to probable kin and social groups in the mind of the researcher.

The results of this study are perhaps most important in that they illuminate the great complexity of the social system of this species of New World arboreal primate, one whose social behavior has previously been depicted as the dependent variable in studies of the ecological setting in which Ateles is found. Hopefully, recognition of the complexity of the social behavior of Ateles geoffroyi, as it has been revealed here, will contribute to future studies of this species as researchers now attempt to gain better

understanding of the intricacies of social behavior of spider monkeys specifically, and primates in general.

REFERENCES

Aldrich-Blake, F. P. G. 1970. Problems of social structure in forest monkeys. In Social Behavior of Birds and Mammals, ed., John Hurrell Crook, pp. 79-101. Academic Press, Inc., (London) Ltd.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49 (3-4): 227-267.

Baldwin, J. D. 1968. The social behavior of adult male squirrel monkeys in a seminatural environment. Folia Primat. 9: 281-314.

Baldwin, J. D. 1969. The ontogeny of social behavior of squirrel monkeys (Saimiri sciureus) in a seminatural environment. Folia Primat. 11: 35-79.

Baldwin, J. D. 1971. The social organization of a semi-freeranging troop of squirrel monkeys (Saimiri sciureas). Folia Primat. 14: 23-50.

Bramblett, Claude. 1976. Patterns of Primate Behavior. Mayfield Publishing Company, California.

Burton, Frances D. 1977. Ethology and the development of sex and gender identify in non-human primates. Acta Biotheoretica 26, 1: 1-18.

Candland, D. K., Tyrrell, D. S., Wagner, D. S., and Wagner, N. M. 1973. Social preference of the squirrel monkey. Folia Primat. 19: 437-449.

Cant, J. 1976. Ecology, Locomotion and Social Organization of Spider Monkeys (Ateles geoffroyi). Ph.D. dissertation, University of California, Davis.

Carpenter, C. R. 1935. Behavior of red spider monkeys in Panama. Jour. of Mammol. Vol. 16, No. 3: 117-179.

Carpenter, C. R. 1958. Territoriality: A review of concepts and problems. In Behavior and Evolution. eds., A. Roe and G. G. Simpson, pp. 224-245. Yale University Press, New Haven.

Carr, Robert F. and Hazard, James E. 1961. Tikal Reports, Number 11, University Museum, University of Pennsylvania, Philadelphia.

Chalmers, N. R. 1973. Differences in behavior between some arboreal and terrestrial species of African monkeys. In Comparative Ecology and Behavior of Primates, ed. R. P. Michael and J. H. Crook, pp. 69-100. Academic Press, London.

Clutton-Brock, T. H. 1974. Primate social organization and ecology. Nature, 250: 539-542.

Clutton-Brock, T. H. and Harvery, P. H. 1976. Evolutionary rules and primate society. In Growing Points in Ethology eds., P. P. G. Bateson and R. A. Hinde, pp. 195-239. Cambridge Univ. Press, Cambridge, England.

Coe, C. L. and Rosenblum, L. A. 1974. Sexual segregation and its ontogeny in squirrel monkey social structure. J. Human Evol. 3: 144-154.

Coelho, A. 1977. Activity patterns in howler and spider monkeys: An application of socio-bioenergetic methods. Working paper presented at the Annual Meeting of the American Association of Physical Anthropologists, April 1977, Seattle, Washington.

Coelho, A., Coelho, L., Bramblett, C., Bramblett, S., and Quick, L. In Press. Ecology, population characteristics and sympatric association in primates: A socio-bioenergetic analysis of howler and spider monkeys in Tikal, Guatemala. Yearbook of Physical Anthropology, Vol. 20. In Press.

Coelho, A., Coelho, L., Bramblett, C., Bramblett, S., and Quick, L. In Press. Resource Availability and Population Density: A Socio-Bioenergetic Analysis of the Energy Budgets of Guatemalan Howler and Spider Monkeys.

Crook, J. H. 1970. The socio-ecology of primates. In Social Behaviour of Birds and Mammals. ed. John Hurrell Crook, pp. 103-166. Academic Press, Inc., (London) Ltd.

Crook, J. H. 1972. Sexual selection, dimorphism and social organization in primates. In Sexual Selection and the Descent of Man. ed. B. Campbell, pp. 231-238. Aldine, Chicago.

Crook, J. H. and Gartlan, J. S. 1966. Evolution of primate societies. Nature 210: 1200-1203.

Devore, I. and Washburn, S. 1963. Baboon ecology and human evolution. In African Ecology and Human Evolution. eds. F. Howell and F. Boivaliere, pp. 335-367. Aldine, Chicago.

Drickamer, L. C. and Vessey, S. H. 1973. Group-changing in free-ranging male rhesus monkeys, Primates 14(4): 350-368.

Durham, N. M. 1971. Effects of altitude differences on group organization of wild black spider monkeys (Ateles paniscus). In Proceedings of the Third International Congress of Primatology, Zurich, S. Carger, A. G. Basel, Switzerland, Vol. 3.

Eisenberg, J. F. 1976. Communication Mechanisms and Social Integration in the Black Spider Monkey Ateles fusiceps and Related Species. Smithsonian Contr. Zoo. 113.

Eisenberg, J. F. and Kuehn, R. E. 1966. The Behavior of Ateles geoffroyi and Related Species. Smithsonian Misc. Collection. 151(8).

Eisenberg, J. F., Muckerhirn, N. A., and Rudran, R. 1972. The relationship between ecology and social structure in primates. Science 176: 863-874.

Erikson, G. E. 1963. Brachiation in New World monkeys and in anthropoid apes. Symp. Zool. Soc. Lond. 10: 135-164.

Fedigan, L. M. 1976. A Study of Roles in the Arashiyama West Troop of Japanese Monkeys (Macaca fuscata). Contributions to Primatology, Vol. 9, S. Karger, A. G. Basel, Switzerland.

Forbes, H. O. 1896. A Handbook to the Primates. Vol. 1. Edward Lloyd, Limited, London.

Freese, Curtis. 1976. Censusing Alouatta palliata, Ateles geoffroyi and Cebus capucinus in the Costa Rica Dry Forest. In Neotropical Primates: Field Studies and Conservation. eds. R. W. Thorington and P. G. Heltne, National Academy of Sciences, Washington, D.C.

Gartlan, J. S. 1968. Structure and function in primate society. Folia Primat. 8: 89-120.

Goodall, J. 1965. Chimpanzees of the Gombe Stream Reserve. In Primate Behavior. ed. I. Devore, pp. 425-473. Holt, Rinehart and Winston, New York.

Harlow, H. F. and Lauersdorf, H. E. 1974. Sex differences in passion and play. Perspect. Biol. Med. 17(3): 348-360.

Hernandez, Camacho, Jorge and Cooper, Robert, W. 1976. The nonhuman primates of Colombia. In Neotropical Primates: Field Studies and Conservation. eds. P. W. Thorington and P. G. Heltne. National Academy of Sciences, Washington, D.C.

Hinde, Robert A. 1974. Biological Bases of Human Social Behaviour. McGraw-Hill, Inc., New York.

Hinde, Robert A. 1976. Interactions, relationships and social structure. Man (N.S.) Vol. 11: 1-17.

Hinde, R. A. and Hinde-Stevenson, J. 1976. Towards an understanding of relationships: dynamic stability. In Growing Points in Ethology. eds. P. P. G. Bateson and R. A. Hinde, pp. 451-479, Cambridge University Press, Cambridge.

Itani, Junichiro. 1977. Evolution of primate structure. J. of Hum. Evol. 6: 235-243.

Jay, Phyllis. 1963. Mother-infant relations in langurs. In Maternal Behavior in Mammals. ed. Harriet L. Rheingold, pp. 282-304. John Wiley & Sons, Inc., New York.

Jensen, Gordon D., Bobbitt, Ruth A., Gordon, Betty N. 1967. Sex differences in the development of independence of infant monkeys. Behaviour : 1-13.

Kellogg, R. and Goldman, F. A. 1944. Review of the spider monkeys. Proceedings of the U.S. National Museum, 96 (3186).

Klein, L. L. 1971. Observations on copulation and seasonal reproduction of two species of spider monkeys, Ateles belzebuth and A. geoffroyi. Folia Primat. 15: 233-248.

Klein, Lewis L. 1972. The Ecology and Social Organization of the Spider Monkeys, Ateles belzebuth. Ph.D. dissertation, University of California.

Klein, Lewis L. 1974. Agonistic behavior in neotropical primates. In Primate Aggression, Territoriality, and nophobia. ed. Ralph Holloway, pp. 77-120. Academic Press, New York.

Klein, Lewis L. and Klein, Dorothy. 1971. Aspects of social behavior in a colony of spider monkeys, Ateles geoffroyi. Int. Zoo. Yearbook 11: 175-181.

Klein, Lewis L. and Klein, Dorothy. 1973. Observations on two types of neotropical primate intertaxa associations. Amer. J. Phys. Anthrop. 38: 649-654.

Klein, Lewis L. and Klein, Dorothy. 1976. Neotropical primates: Aspects of habitat usage, population density, and regional distribution in La Macarena, Colombia. In Neotropical Primates: Field Studies and Conservation. eds. R. W. Thorington and P. G. Heltne. National Academy of Sciences, Washington, D.C.

Kling, A. and Steklis, H. D. 1976. A neural substrate for affiliative behavior in non-human primates. Brain Behav. Evol. 13: 216-238.

Koyama, Naoki. 1973. Dominance, grooming, and clasped-sleeping relationships among bonnet macaques in India. Primates 14, (2-3): 225-244.

Kummer, Hans. 1971. Primate Societies: Group Techniques of Ecological Adaptation. Aldine, Chicago.

Lancaster, J. B. 1973. In praise of the acheiving female monkey. Psychology Today 7, 30-37.

Lancaster, J. B. 1976. Sex roles in primate societies. In Sex Differences. ed. Michael S. Teitelbaum, Anchor Press, Doubleday.

Lundell, C. 1937. The Vegetation of the Peten. Carnegie Institute of Washington. Washington, D.C.

Marler, P. 1969. Colobus guereza: Territoriality and group composition. Science, 163: 93-95.

Mason, W. A. 1964. Sociability and social organization in monkeys and apes. In Recent Advances in Experimental Psychology. ed. L. Berkowitz, pp. 277-305. Academic Press, New York.

Mason, W. A. 1976. Primate social behavior: Pattern and Process. In Evolution of Brain and Behavior in Vertebrates. eds. Masterton et al., pp. 425-455. Lawrence Erlbaum Associates. Hillsdale, New Jersey.

Mason, W. A., Green, P. C. and Posepanko, C. J. 1960. Sex differences in affective social responses of rhesus monkeys. Behaviour, Vol. 16: 74-83.

Mayr, Ernst. 1972. Sexual selection and natural seclection. In Sexual Selection and the Descent of Man. ed. Bernard Campbell. pp. 87-104. Aldine, Chicago.

Missakian, E. A. 1973. The timing of fission among free-ranging rhesus monkeys. Am. J. Phys. Anthropol., 38: 621-624.

Mitchell, G. and Tokunaga, D. H. 1976. Sex differences in nonhuman primate grooming. Behavioural Processes, 1: 335-345.

Mittermeier, R. A. and Fleagle, J. G. 1976. The locomotor and postural repertoires of Ateles geoffroyi and Cebus guereza, and a re-evaluation of the locomotor category semibrachiation. Am. J. Phys. Anthrop. 45: 235-256.

Napier, J. R. and Napier, P. H. 1967. A Handbook of Living Primates. Academic Press, New York.

Nishida, Toshisada. 1966. A sociological study of solitary male monkeys. Primates, Vol. 7, No. 2: 141-204.

Poirier, F. E. 1968. Nilgiri langur (Presbytis johnii) Territorial behavior. Proc. 2nd Int. Congr. Primat., New York.

Quick, Larry Beaumont. 1974. Activity Patterns and Behavior of the Spider Monkey at Tikal, Guatemala. unpublished Masters Thesis, University of Texas at Austin.

Ralls, Katherine. 1976. Mammals in which the females are larger than males. The Quarterly Review of Biology, Vol. 51: 245-276.

Ransom, R. W., and Ransom, B. S. 1971. Adult male-infant relations among baboons (Papio anubis). Folia Primatol. 15: 179-195.

Redican, William K. 1976. Adult male-infant interactions in non-human primates. In The Role of the Father in Child Development. ed. Michael E. Lamb, pp. 345-385. John Wiley & Sons, Inc., New York.

Reynolds, Vernon. 1970. Roles and role change in monkey society: The consort relationship of rhesus monkeys. Man 5: 449-465.

Richard, Alison. 1970. A comparative study of the activity patterns and behavior of Alouatta villosa and Ateles geoffroyi. Folia Primat. 12: 241-263.

Rondinelli, Robert and Klein, Lewis L. 1976. An analysis of adult social spacing tendencies and related social mechanisms in a colony of spider monkeys (Ateles geoffroyi) at the San Francisco Zoo. Folia Primat. 25: 122-142.

Rose blum, Leonard. 1974. Sex differences, environmental complexity and mother-infant relations. Archives of Sexual Behavior, Vol. 3, No. 2: 117-128.

Rowell, T. E. 1974. Contrasting adult male roles in different species of nonhuman primates. Archives of Sexual Behavior, Vol. 3, No. 2: 143-149.

Rowell, R. E., Din, N. A. and Omar, A. 1968. The social development of baboons in their first three months. J. Zool. 155: 461-483.

Sade, D. 1965. Some aspects of parent-offspring relations in a group of rhesus monkeys, with a discussion of grooming. Am. J. Phys. Anthrop., 23: 1-18.

Siegel, Sidney. 1956. Nonparametric Statistics for the Behavioral Sciences. New York: McGraw-Hill.

Simonds, Paul E. 1974. Sex differences in bonnet macaque networks and social structure. Archives of Sexual Behavior, Vol. 3, No. 2: 151-166.

Struhsaker, T. T. 1969. Correlates of ecology and social organization among African cercopithecines. Folia Primat. 11: 80-118.

Wagner, H. O. 1956. Freilanbeobachtungen an Klmmeraffen Zeitschrift fur Tierpsychologie 13(2): 302-313.

Young, G. H. and Hankins, R. J. 1977. Paternal influences on the development of behavioral sex differences in infant baboons. Paper presented at 46th Annual Meeting of the American Association of Physical Anthropologists, Seattle, Washington.

APPENDIX ONE

DATA SHEET

Subject: AF Date: 3/3/78 Time: 14:58

Context: Large mixed association foraging east of Temple IV (quadrant 05)

Proximity: AF, AF, JM, JF, Mother and Infant Female (Adult males - 4, left area 14:55)

Time	Action	Direction	Object	Comments
0	eat	--		zapote fruit
34	app	→	JF	(previously noted in association with subject)
38	sic	↔	JF	
243	brc	→	JF	leaves to feed in neighboring ramon tree
244	sit	—		Subject remains sitting
300				Subject still sitting, foraging in area continues quietly. Proximity same

APPENDIX TWO

ETHOGRAM

1. EAT: Foraging behavior involving any activity aimed at locating, obtaining or eating food. This was only recorded when no other behavior involving social interaction could be heard or seen. For example it is interrupted by any form of vocalization, such as CONTACT CALL.

2. LOC: Locomote refers to any form of movement from one location to another, more than 1 meter away and longer than 5 secs. in duration. Thus brachiation, branch running and walking, leaping, are all subsumed in this action. The behavioral categories of FOLLOW, CARRY, RETREAT, CHASE APPROACH, BRIDGE, all of which also describe locomotion qualitatively are used instead of LOCOMOTE if they are clear to both observers.

3. SIT: Sit refers to a stationary position and it includes hanging, sitting or lying. As the previous two behaviors, Sit is only recorded in the absence of other forms of activity defined in this ethogram. Thus SIT IN CONTACT, SIT BESIDE, EMBRACE, etc., replace SIT.

4. COC: Contact call refers to a vocalization which is either elicited by or elicits a vocalization by one or more other individuals. This vocalization may be any form of vocalization established between individuals and that this is apparent to the observer by the answering vocalization.

5. VOC: Vocalization refers to a sound made by an individual which does not fall into the categories: PLAY VOCALIZATION, YELP, AGONISTIC BARK, GROWL, DISTRESS BARK, WHINE, or GRUNT. It is generally a very common whinny sound, and is neither elicited by, nor does it elicit a response. However, a vocalization may be directed at another individual, recorded as object if this is clear to both observers.

6. FOL: Follow refers to locomotion of one individual behind another, with clear intentions of 'following' another monkey. The decision to call such a behavior 'follow' is made using these criteria: 1. previous contact of animals and certain behaviors such as waiting for and looking back at follower. 2. spacing between monkeys and/or similarity of arboreal pathways being used. 3. direct communication between individuals during the sequence.

7. APP: Approach refers to locomotion of one individual towards another, to within at least 3 m. Intent on the part of the approaching monkey need not be shown. Contact may or may not subsequently be established between the individuals concerned.

8. RET: Retreat refers to behavior in which one individual rapidly moves away from another. This does not involve actual physical contact as does ATTACK, nor is it as directly agonistic as CHASE. Generally the retreating monkey does so before it has occasion to be chased, and RETREAT is not as immediate or obvious as DISPLACE.

9. EMB: Embrace refers to two (or more) individuals sitting or lying together. Not only are they in close body contact but some form of embrace is evident. Closer, more intense contact involving arm and leg intertwinning distinguish EMBRACE from SIT IN CONTACT.

10. PSE: Pectoral Sniff and EMBRACE refers to a taxa specific behavior described by Klein for Ateles belzebuth in Colombia. Usually seen in a greeting context, this action involves a fairly stereotypic motor pattern of mutual embracing with a concomitant sniff of pectoral and/or genital regions by the individuals. This is often accompanied by a whinny vocalization which is not recorded separately (Klein 1972).

11. CHR: Chest Rub refers to another fairly stereotyped motor pattern in which an individual rubs or scratches his/her chest or abdominal region with the tips of the fingers.

12. ARR: Arm Rub refers to a behavior which, like chest rubbing is more than a relaxed scratching motion. It is a strong downward stroke of the hand on the arm.

13. TOU: Touch refers to a 'touch' of one animal by another, usually by placing the forearm or hand on the other. No apparent agonism is intended, nor is this a part of either GROOM or PLAY bout.

14. GRO: Groom is a fairly self-explanatory behavior, in which one individual grooms another. Intervals of 5 seconds during which grooming is briefly stopped are not recorded. This can be either self-directed or allo-grooming.

15. SOG: Solicit Groom refers to one individual presenting some part of his/her body to another for grooming. Usually this involves lying directly in front of another individual, lifting the arm vertically and exposing the ventrum. SOLICITING GROOM in this way may or may not be followed by grooming.

16. PLC: Play Chase refers to a sequence of chasing which occurs within a play context, and is at least 5 seconds in duration. Play context of this behavior distinguishes it from CHASE, which occurs in agonistic situations.

17. PLV: Play Vocalization refers to a low coughing sound which is described by Eisenberg (1976) as an ook-ook sound. This usually accompanies bouts of PLAY or GRAPPLE.

18. LEA: Leap as a separate category from locomote was deleted after it became clear to the observers that their ability to judge distances which would mark LEAPS was severely limited.

19. NUR: Nurse as a behavior is self-explanatory. This activity was limited to the three age-sex categories: infant male, infant female, and mother of infant.

20. SRA: Scratch refers to a very common motor pattern, in which an individual uses his/her forearm or hindlimb to scratch any part of the body. This is a much more leisurely movement than either ARM RUB or CHEST RUB, and often seems to be a pattern accompanying both nervousness and relaxation. It is distinguished as well from GROOM, since the area being scratched is not scrutinized or picked at. Usually self-directed.

21. SIC: Sit In Contact refers to sitting, lying or hanging of two or more monkeys together and maintaining some body contact with each other. No EMBRACE is evident, nor are any other forms of interactions such as GROOM, NURSE, COPULATE taking place if Sit In Contact is recorded.

22. CAR: Carry refers to an activity almost entirely restricted to infants and mothers, in which the subject is either being carried by, or carrying another on the dorsum or ventrum during locomotion.

23. DIS: Displace refers to the displacement of one individual by another in a clear incidence where one moves very close to another and replaces it directly. It is distinguished from APPROACH RETREAT by the rapidity with which it occurs and the proximity of the monkeys to each other when the displacement takes place.

24. LOO: Look Around refers to a very broad spectrum of behaviors which involves the subject directing his/her attention at some other monkeys, the researchers, noises, or just around. The look in no way belies intention such as THREAT, and yet it is more than just a glance. Generally this reveals a visual alertness which follows, or is followed by some other activity pattern.

25. GET: Genital Touch refers to an activity in which the subject touches either his/her own genitals without any apparent scratching motion, or touches those of another monkey.

26. FIS: Finger Sniff is also a self-explanatory motor pattern, usually performed by a male monkey after touching the genitalia of a female.

27. BRS: Branch Sniff refers to a very obvious sniffing action of a branch or an entire area in a tree where the individual performs it. No direction or object is recorded for this although this is often seen performed by males after a female moves away.

28. BSH: Branch-Shake refers to a taxa specific display in which an individual bounces, shakes, or breaks branches. If the display occurs with no apparent motive no object is recorded. Usually, however, this behavior is directed at some other monkey and is especially prevalent when the researchers seem to be upsetting a group of monkeys. This is distinguished from a more specific type of display which is recorded separately as DISPLAY HOWL, due to the accompanying vocalization and higher intensity of the latter.

29. OMT: Open Mouth Threat refers to an entire facial expression in which an individual opens its mouth in an 'o' formation and stares at another (or the researchers) in a threatening way. The face is very tense and this expression is usually made either before, after or during an interlude in a sequence of BRANCH SHAKING.

30. BRC: Break Contact refers to a cessation of any of the following: SIT IN CONTACT, SIT BESIDE, EMBRACE, EAT IN CONTACT, PECTORAL EMBRACE AND SNIFF, GROOM, (if SIT IN CONTACT is broken when GROOM ceases), GRAPPLE, CARRY, COPULATE, NURSE. If the initiator of the separation is obvious to the researchers, this is recorded. Otherwise the behavior is recorded as being mutual in direction. This behavior is recorded only if the change in proximity or behavior does not involve any other actions such as CHASE, PLAY CHASE, RETREAT. If a subject does not BREAK CONTACT, FOLLOWING may then ensue.

31. GRA: Grapple refers to a characteristic form of wrestling, with intensive body contact, but in non-agonistic contexts. Eisenberg (1976) describes GRAPPLE as a form of mock-fighting with play bitting. As well it usually seems to take place most typically when individuals are hanging by their tails, and uttering PLAY VOCALIZATIONS. As many as 6 monkeys may be involved in one GRAPPLING bout.

32. YEL: Yelp refers to a very characteristic vocalization which is made with a very rounded mouth, and a steady high-pitched type of calling. At each YELP a strong expulsion of breath is made, and YELPING may continue in bouts lasting over an hour.

33. SIB: Sit Beside refers to a neutral position in which two or more individuals are sitting in extremely close proximity to each other but are not in actual contact. There may be one or more individuals SITTING IN CONTACT at the same time, and in this case both SIT BESIDE and

SIT IN CONTACT are recorded concomitantly for the subject. This merely records proximity of monkeys. If one individual approaches another and sits beside then he/she is recorded as the initiator. If the proximity appears to have been established by both individuals, or is continuous the direction is recorded as being mutual.

34. PLA: Play refers to immediately non-functional activities by or between individuals. It is especially characteristic of young monkeys alone in a tree, or between peers.

35. GRU: Grunt refers to a suppressed type of vocalization which involves a short 'grunting' sound. This often either precedes or follows a bout of YELPING.

36. DRI: Drink is a self-explanatory motor pattern. For spider monkeys this usually involves scooping water from a crook in a tree with the hand.

37. URI: Urinate is also self-explanatory.

38. DEF: Defecate is also self-explanatory.

39. AGB: Agonistic Bark refers to a short rather sharp bark sound which is emitted in situations of high agonism. This may take the form of a shriek but is not a GROWL or DISTRESS BARK. Context serves to aid in identification of this vocalization.

40. GRW: Growl refers to very low gutteral growling sound which is heard in agonistic encounters. Often heard before, during or after a sequence of CHASING.

41. EIC: Eat in Contact refers to two animals maintaining bodily contact as they eat. This category was only seen when mothers and infants were being observed. Often either or both mother and infant would eat while maintaining contact. Direction for this behavior indicates who is doing the eating. For example, if the mother is eating while the infant sits quietly on her back, the initiator of the activity is the mother, the infant is the receiver. If both are eating the activity is recorded as mutual.

42. ERE: Erection refers to the erection of the male penis. This is only recorded if it is clearly visible. If the researcher can no longer see the genitalia, the activity is not recorded. Usually recorded simultaneously with another form of behavior, such as GROOM, SIT IN CONTACT, SIT BESIDE.

43. TER: Terrestrial Behavior originally was devised to record incidences in which the monkeys came to the ground for some reason, usually to the side of a temple to eat limestone, or to play. This category was subsequently deleted due to the fact that only once was an animal seen on the

ground, and this was only for a few seconds when chased. Secondly it was realized that the tops of temples were simply extensions of arboreal pathways for the monkeys and that visibility was poor for the researchers when monkeys were on these.

44. BRI: Bridge refers to an activity in which one individual uses his/her own body to join branches of adjacent trees to permit easier passage for another, who uses this "bridge". Usually performed by mothers of slightly older infants who are able to make their way slowly through the trees, but are by no means independent of their mothers.

45. DIB: Distress Bark refers to a sharp, shriek-like vocalization resembling a cry of fear or distress. This is especially common in sequences of highly agonistic behavior and usually heard from monkeys who have just been CHASED, ATTACKED, or are RETREATING. As well this cry is often heard by monkeys alone and apparently 'looking for' certain others.

46. CHA: Chase refers to rapid and overtly agonistic chase of one animal by another. This may be a full scale chase for many meters through the trees, or a short lunging advance, but no physical contact occurs as in ATTACK. (Often accompanied by DISTRESS BARK if the individual is being chased, and AGONISTIC BARKS if the individual is doing the chasing).

47. WHI: Whine refers to a very high-pitched whining sound without the loud shrillness of Barks. It may resemble a mewing sound and is often heard by infants and juveniles communicating with mothers and adult females. As well it frequently occurs after agonistic encounters.

48. BRR: Branch Rub refers to any movement in which an individual apparently rubs either genitalia or the pectoral region on a branch. A female, for example rubs her long clitoris along a branch by sliding down the limb. This may have some marking function as indicated by the PLACE OR BRANCH SNIFFING which frequently follows BRANCH RUB.

49. AGA: Agonistic Approach was originally devised to record approaches which did not enhance affinity between individuals. However, this category was deleted since such approaches usually involved either CHASING or resulted in DISPLACE.

50. COP: Copulate refers to activity which involves thrusting by the male and reception by the female.

51. ATT: Attack refers to an encounter between two or more monkeys which is more severe than CHASE since it involves actual cuffs, hits, or swipes at other animals.

52. SPA: Spar refers to a behavioral sequence in which individuals do not actually come in to contact for wrestling, or playing and yet they do not CHASE or RETREAT from each other as in agonistic situations. Instead this involves a sort of teasing in which they circle each other and maintain a fairly even distance between themselves, only seen between spiders and howlers.

53. DIH: Display Howl refers to form of ritualized display behavior which is most often exhibited by several adult males together. Eisenberg refers to this as a "Male agonistic display" (1976). It involves leaping, branch-shaking, physical contact between males as they perform the display and loud howling which may be a form of intergroup spacing behaviors.